

Research Article

Phonological Working Memory for Words and Nonwords in Cerebral Cortex

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Purpose: The primary purpose of this study was to identify the brain bases of phonological working memory (the short-term maintenance of speech sounds) using behavioral tasks analogous to clinically sensitive assessments of nonword repetition. The secondary purpose of the study was to identify how individual differences in brain activation were related to participants' nonword repetition abilities.

Method: We used functional magnetic resonance imaging to measure neurophysiological response during a nonword discrimination task derived from standard clinical assessments of phonological working memory. Healthy adult control participants ($N = 16$) discriminated pairs of real words or nonwords under varying phonological working memory load,

which we manipulated by parametrically varying the number of syllables in target (non)words. Participants' cognitive and phonological abilities were also measured using standardized assessments.

Results: Neurophysiological responses in bilateral superior temporal gyrus, inferior frontal gyrus, and supplementary motor area increased with greater phonological working memory load. Activation in left superior temporal gyrus during nonword discrimination correlated with participants' performance on standard clinical nonword repetition tests.

Conclusion: These results suggest that phonological working memory is related to the function of cortical structures that canonically underlie speech perception and production.

The cognitive processes that underlie the short-term maintenance of language sounds are known collectively as *phonological working memory*. Phonological working memory is thought to support a wide range of linguistic behaviors, including novel word learning and vocabulary development, maintenance of information during sentence and discourse processing, and the acquisition of reading skill (Adams & Gathercole, 1995, 1996; Baddeley, Gathercole, & Papagno, 1998; Dufva, Niemi, & Voeten, 2001; Gathercole & Baddeley, 1993; Hasselhorn & Körner, 1997; Martin, 2005; van der Schuit, Segers, van Balkom, & Verhoeven, 2011). Despite the broad behavioral relevance of phonological working memory in language development and processing, little is known about the brain bases of this ability, particularly with respect to how it has been operationalized and assessed clinically via tests of nonword repetition. Moreover, the prevalence of phonological working

memory impairments in individuals with developmental disorders of language and communication demands a better understanding of the psychological and neurobiological processes underlying the short-term maintenance of verbal information in order to better understand the etiology of these impairments.

Deficits in phonological working memory occur in a number of developmental disorders of language and communication. *Specific language impairment* (SLI), for instance, is characterized by a profound phonological working memory deficit (Conti-Ramsden, Botting, & Faragher, 2001; Ellis Weismer et al., 2000; Graf Estes, Evans, & Else-Quest, 2007). Individuals with Down syndrome exhibit a similar set of linguistic deficits to those with SLI, including prominently a deficit in phonological working memory (Lanfranchi, Jerman, & Vianello, 2009; Laws & Bishop, 2003). Although not diagnostic of the disorder, phonological working memory impairment is frequently observed in individuals with developmental dyslexia (e.g., Larrivee & Catts, 1999; Peter et al., 2011) and is related to other phonological measures prior to the onset of reading instruction (Clark, McRoberts, Van Dyke, Shankweiler, & Braze, 2012). Children and adults who stutter also appear to have deficits in phonological working memory that may be independent of speech fluency (Anderson, Wagovich, & Hall, 2006; Byrd, McGill, & Usler, 2015; Hakim & Ratner, 2004). In autism, too,

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Editor: Sean Redmond

Associate Editor: Michael Dickey

Received December 29, 2015

Revision received May 25, 2016

Accepted October 27, 2016

https://doi.org/10.1044/2017_JSLHR-L-15-0446

Disclosure: The authors have declared that no competing interests existed at the time of publication.

there is a pronounced impairment in phonological working memory (Kjelgaard & Tager-Flusberg, 2001), which appears to extend even to first-degree family members evincing the broad autism phenotype (Wilson et al., 2013).

The relationship between phonological working memory and language abilities has been most clearly demonstrated in developmental communication disorders through clinical assessments of nonword repetition abilities (e.g., Dollaghan & Campbell, 1998; Gathercole, Willis, Baddeley, & Emslie, 1994; Wagner, Torgesen, & Rashotte, 1999). In these tests, individuals listen to unfamiliar spoken items and are prompted to repeat them aloud. Phonological working memory, measured by nonword repetition, taps core speech perception and linguistic processes of encoding, storage, and production while eschewing the additional contribution of semantics and item familiarity to performance on typical digit-span or word-list serial recall tasks. In this way, nonword repetition may provide a more parsimonious measure of core phonological processing demands than canonical verbal short-term memory tasks (Gathercole et al., 1994). In developmental communication disorders, individuals may perform accurately for one- or two-syllable nonwords but tend to make increasingly more errors relative to age-matched typically developing children or adults as the number of syllables (or the phonological working memory load) increases (Byrd, Vallely, Anderson, & Sussman, 2012; Gathercole & Baddeley, 1990; Gathercole et al., 1994; Graf Estes et al., 2007; Montgomery, 1995; Riches, Loucas, Baird, Charman, & Simonoff, 2011; Wagner et al., 1999).

There have been many studies of the brain bases of verbal working memory as measured by classical digit-span or word-list serial recall tasks used in cognitive psychology (reviewed in Buchsbaum & D'Esposito, 2008). Early neuroimaging studies of auditory short-term memory originally implicated areas in parietal lobe as the putative locus for short-term storage of phonological information (Awh et al., 1996; Baddeley, 2003; Paulesu, Frith, & Frackowiak, 1993; E. E. Smith, Jonides, & Koeppe, 1996). However, subsequent studies have increasingly found evidence for an alternative locus for this ability in superior temporal cortex, particularly posterior planum temporale (e.g., Buchsbaum, Olsen, Koch, & Berman, 2005). A variety of methodological approaches now provide converging lines of evidence for the idea that superior temporal cortex is a critical component of the cortical network underlying phonological working memory on the basis of its operationalization in cognitive psychology. Superior temporal cortices are now routinely implicated in functional neuroimaging studies of auditory short-term memory (e.g., Buchsbaum et al., 2005; Strand, Forssberg, Klingberg, & Norrelgen, 2008), and anatomical neuroimaging studies have found correlations between the macro-anatomical structure of the superior temporal cortex and verbal working memory capacity in individuals with both language-impaired and developmentally typical profiles (Lu et al., 2016; Richardson et al., 2011). These results parallel growing evidence from large-sample studies of auditory short-term memory deficits following brain injury, which specifically attribute this impairment to lesioned tissue in

left superior temporal cortex (Koenigs et al., 2011; Leff et al., 2009). Transcranial magnetic stimulation (TMS) applied to left posterior superior temporal gyrus (STG) has also been shown to interfere in the maintenance of nonwords in short-term memory (Acheson, Hamidi, Binder, & Postle, 2011). However, there has been little direct examination of how tasks such as nonword repetition, which are most clinically sensitive for phonological working memory impairments in developmental communication disorders, are supported by the brain.

It is particularly important to identify the brain areas that exhibit scaling responses to the increased phonological working memory demands of longer versus shorter nonwords, because it is the heightened memory demands of long nonwords that appear to be most challenging to, and have the greatest diagnostic specificity for, individuals with developmental language disorders (Graf Estes et al., 2007). More knowledge about the profile of brain regions that are responsive to nonwords of increasing length is therefore necessary not only to inform basic research questions concerning the neural correlates of phonological working memory, but also to potentially better understand the etiology of phonological working memory deficits in the many clinical disorders of language and reading in which such deficits are observed. For instance, the observation that greater phonological working memory loads increasingly recruit regions associated with speech perception (such as superior temporal cortex), speech production (such as motor and premotor cortices), or domain-general working memory and executive control (such as dorsolateral prefrontal cortex), would differentially suggest that phonological working memory impairments may arise from problems with encoding and representation, interruptions to rehearsal and sequencing, or limitations on nonlinguistic resource allocation, respectively. Identifying the area or network of areas that supports the increasing demands of phonological working memory in a healthy, mature context can thus provide a framework for exploring dysfunction of these areas in developmental language disorders, which, in turn, may help inform the selection of more targeted, efficacious strategies for remediation of these deficits.

In this study we used functional magnetic resonance imaging (fMRI) to assess the neural systems underlying phonological working memory that are activated during an in-scanner nonword discrimination task, and to assess their relationship to performance on out-of-scanner nonword repetition tests. Nonwords of increasing length were used to parametrically manipulate phonological working memory load (operationalized by the number of syllables)—an approach frequently used in studies of phonological working memory impairments in developmental language disorders (Graf Estes et al., 2007). To avoid motion artifacts associated with speech production in a scanner, we developed a nonword discrimination task in which participants heard target nonwords, maintained them briefly in working memory, and then responded whether the target nonword was the same as or different from a probe nonword. Although clinical assessments typically involve overt

repetition, nonword discrimination serves as a suitable and robust proxy for assessing phonological working memory: Nonword discrimination and repetition abilities are significantly correlated in both typically developing children and adults and children and adults with language impairments (Reuterskiöld-Wagner, Sahlén, & Nyman, 2005; Rispen & Baker, 2012; Van Bon & Van Der Pijl, 1997); nonword discrimination abilities are significantly impaired in individuals with developmental language disorders (Loucas et al., 2010; Montgomery, 1995; Nithart et al., 2009; Szenkovits & Ramus, 2005); and neural responses during nonword discrimination differ between adults with high and low nonword repetition abilities (Barry, Hardiman, & Bishop, 2009). Last, we also included a corresponding task using real words of various lengths as a control condition to gauge how the increased neurophysiological demands of nonword stimuli specifically reflected increasing phonological working memory load as opposed to the increased perceptual demands of encoding longer stimuli.

There are several potential advantages to our approach compared with previous neuroimaging studies of verbal working memory. Unlike studies using tasks analogous to those in classical cognitive psychology research (particularly maintenance of strings of digits, letters, or serial-recall of word lists; e.g., Jonides et al., 1997; Petrides, Alivisatos, Meyer, & Evans, 1993), the phonological working memory task we implemented was more closely analogous to those used clinically in terms of both the design of its stimuli and the timing of participants' responses (cf. Strand et al., 2008). The intention of using a task derived from these clinical measures is to better identify the brain areas supporting the cognitive processes for which such tasks are diagnostically sensitive. In addition, the use of a sparse-sampling fMRI acquisition sequence allowed participants to accurately hear the words and nonwords in the absence of acoustic scanner noise.

Using this nonword/real-word discrimination task, we posed a number of questions: (a) What brain areas are activated by nonword discrimination, and how do these differ from those activated by real-word discrimination? We hypothesized that both nonword and real-word discrimination would recruit perisylvian temporal and frontal regions classically associated with speech perception and production. (b) What brain regions exhibit scaling responses to the increased phonological working memory demands of nonwords of increasing length, and how does response in these regions differ for increasingly longer real words? We hypothesized that discriminating longer real words would recruit superior temporal regions associated with speech perception, corresponding to the greater perceptual demands of these stimuli, whereas discriminating longer nonwords would recruit a wider network of not only superior temporal regions involved in encoding and representation, but also frontal and motor regions potentially involved in the sequencing and subvocal rehearsal of speech. An alternative possibility is that greater phonological working memory load would increasingly recruit areas associated with domain-general attention, memory, and resource allocation, such

as dorsolateral prefrontal cortex. (c) In what areas does activation during nonword discrimination relate to performance on standard clinical assessments of nonword repetition? We hypothesized that brain-behavior correlations between nonword processing and phonological working memory ability would be found in left superior temporal gyrus, consistent with mounting evidence from lesion studies that this area is critically involved in phonological working memory. A core phonological working memory network, identified from converging evidence across these three lines of inquiry, will provide a framework for future studies of the brain bases of phonological working memory impairments in developmental language disorders.

Method

Participants

Sixteen adult participants (seven men, nine women; aged 18–32 years, $M = 25.4$ years) successfully completed this study. Although nonword repetition deficits are often observed in children with developmental communication disorders, we recruited adult participants with a developmentally typical background in order to ascertain the neural correlates of the intact, mature phonological working memory system. Participants were, by self-report, right-handed native speakers of American English who had no lifelong history of speech, hearing, reading, or language difficulties (and no family history of the same), no history of cognitive or motor developmental difficulties, no known neurological or psychiatric disorders, and were not currently taking medication affecting the nervous system. Participants reported having between 1 and 9 years of postsecondary education ($M = 5$ years). This study was approved by the Massachusetts Institute of Technology Committee on the Use of Humans as Experimental Subjects; participants provided informed, written consent and received monetary compensation for their time.

Neuropsychology: Behavioral Assessments

Participants completed a brief battery of standardized clinical measures of cognitive and linguistic ability, including the Kaufman Brief Intelligence Test (expressive vocabulary, definitions, and matrix subtests; Kaufman & Kaufman, 1990), the Comprehensive Test of Phonological Processing (CTOPP; Elision, Blending Words, and Nonword Repetition subtests; Wagner et al., 1999), and the Children's Test of Nonword Repetition (CNRep; Gathercole & Baddeley, 1996; Gathercole et al., 1994).

Phonological awareness tasks, such as CTOPP Elision and Blending Words, are typically used to assess language and reading-related skills in children and adults with developmental learning disorders. These tasks require participants to remove sound segments from words to produce other words ("say *cat* without saying [k]") or to combine separate sounds into their composite word ("say [k] [æ] [t] as one word"). Phonological working memory tasks, such as CTOPP nonword repetition and CNRep, are typically used to diagnose

children at risk for language disorders such as SLI and require participants to listen to recordings of nonwords of varying length (e.g., CNRep: two to five syllables; CTOPP: three to 15 phonemes) and repeat them orally. The CNRep test as published consists of recordings produced by a British English speaker. For the present study, the recordings were reproduced by an adult female native speaker of American English, with careful attention to maintaining the intended phonemic constituents but with standard American pronunciation.

Stimuli

Real-word stimuli consisted of 90 pairs of English words, distributed equally across three phonological working memory levels (stimuli of lengths: two, four, and six syllables). Each syllable level included 15 pairs of matching words (e.g., *treaty* / *treaty*) and 15 pairs of nonmatching words (e.g., *retreat* / *revenge*), resulting in 135 total unique words. Phonotactics (phoneme and biphone positional probabilities) did not differ between the syllable levels, both $F(1, 133) < 0.92, p > .34$ (Vitevitch & Luce, 2004).

Nonword (*pseudoword*) stimuli were generated that closely paralleled the structural and statistical properties of real English words. Ninety pairs of nonwords were distributed equally across three phonological working memory levels (stimuli of lengths: two, four, and six syllables). Each syllable level included 15 matching pairs (e.g., *klamic* / *klamic*) and 15 nonmatching pairs (e.g., *bicket* / *bippet*), resulting in 135 total unique nonwords. The differences in nonmatching pairs were accomplished through changes designed to replicate the types of production errors observed in children with language impairments during nonword repetition tasks: deletion of a single phoneme (e.g., *tector* / *tetor*), replacement of a single phoneme (e.g., *shoken* / *shopen*), or transposition (metathesis) of a pair of phonemes (e.g., *kolite* / *kilote*). Each of these changes occurred equally often, and affected both consonants and vowels (except in the case of deletion, which was not applied to vowels in order to preserve the number of syllables); changes were never applied to word-initial phonemes due to the salience of these sounds, and the word-medial position of these changes varied so that listeners could not predict where differences might occur. Full lists of the real word and nonword stimuli are available in Appendix A, and a table of the types of phonological manipulations in the nonword pairs is available in Appendix B. Nonword phonotactics (positional phoneme and biphone positional probabilities) did not differ between the syllable levels, both $F(1, 133) < 0.23, p > .61$. There were also no differences between the real-word and nonword stimuli in terms of number of phonemes or phonotactic probabilities, nor interactions between these variables, condition, and syllabic length, all $F(1, 266) < 1.39, p > .23$. Controlling the phonotactic probability of stimuli across the load and lexicality manipulations was important given previous reports that certain cortical language areas are sensitive to this feature (Vaden, Piquado, & Hickok, 2011).

In addition, we compared the phonotactic probability of our real-word and nonword stimuli to those of the

CTOPP and CNRep clinical nonword repetition tests. Analyses of variance of fixed-effects linear models of phoneme and biphone probability given stimulus set and number of syllables revealed a significant effect of stimulus set (phonemes: $F[3, 322] = 12.86, p < 6 \times 10^{-8}$; biphones: $F[3, 322] = 16.95, p < 4 \times 10^{-10}$), such that CTOPP nonwords were significantly less wordlike than the other two sets. Models including only the CNRep and real/nonwords used in the present experiment revealed no differences among stimulus sets (phonemes: $F[2, 306] = 0.74, p = .48$; biphones: $F[2, 306] = 0.74, p = .48$). There were no other main or interaction effects in these comparisons.

Audio recordings of the real-word and nonword stimuli were produced from the speech of a female native speaker of standard American English who was extensively familiarized with the nonwords to ensure natural, correct pronunciation. Stimuli were read in citation format (individually and in isolation) and were digitally recorded using a SM58 microphone (Shure Inc., Niles, IL) and Edirol UA-25EX sound card (Roland Corp., Los Angeles, CA), sampling at 44.1 kHz. Each token was normalized for root-mean-square amplitude to 70 dB using Praat (Boersma, 2001).¹

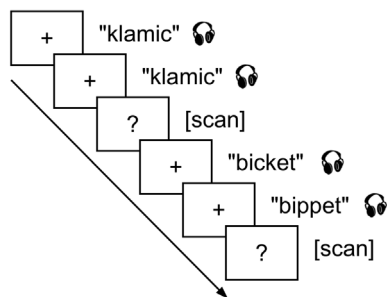
Procedure

Participants' task in the scanner was to listen to pairs of real words or nonwords and indicate, for each pair, whether the two items were identical. Prior to scanning, participants practiced the task using eight example pairs of real words and nonwords that did not occur during the actual MRI session. Participants lay supine in the MRI scanner, held a response box in their right hand, and observed a projected computer display via an angled mirror suspended in front of their eyes. Auditory stimuli were presented binaurally using pneumatic ear-insert phones (Etymotic Research, Elk Grove Village, IL) at a comfortable listening level. Stimulus presentation was controlled by the software E-Prime v1.1 (Psychology Software Tools Inc., Pittsburgh, PA).

Participants underwent two experimental runs, with a duration of 10.8 min each. Each run consisted of 90 trials, equally distributed among the three syllable levels. Trials were organized such that two trials of the same condition/level occurred sequentially (see Figure 1). The order of trial types was randomized and intermixed with 18 rest trials during which no auditory stimuli were presented and no task was performed. The beginning of a trial was indicated by the appearance of a white fixation cross on the black screen, which was present for the duration of the trial. Each trial was 6 s long; stimulus pairs were presented during the 4 s of silence during the sparse delay, followed by 2 s of acoustic scanner noise accompanying functional image acquisition. There was a 1-s interstimulus interval between the end of the first and beginning of the second in each pair. Although many classical neuroimaging studies of verbal working memory utilize long delays between target and

¹Praat: <http://www.fon.hum.uva.nl/praat/>

Figure 1. Task design. Participants discriminated pairs of words or nonwords in an event-related, sparse-sampling functional magnetic resonance imaging (fMRI) design. Pairs of audio stimuli were played during the 4-s silent delay between repetition times (TRs), indicated here by headphones and example nonword stimuli in quotes. No stimuli were presented during the 2-s image acquisition (indicated by [scan]), whereupon participants were prompted to respond via button press.



probe, clinical tests of nonword repetition require individuals to provide an immediate response. Therefore, we chose this short interstimulus interval so that our fMRI results would better reflect the neural processes underlying phonological working memory assessments as they are performed clinically (with immediate repetition), and therefore as they have bearing on developmental communication disorders. A question mark replaced the fixation cross during the last 2 s of each trial, indicating the participant should respond. Dependent measures consisted of participants' neurophysiological response (blood oxygenation level dependent functional time series), behavioral accuracy, and behavioral response time.

MRI Data Acquisition

Data were acquired on a Siemens Trio 3T scanner (Siemens AG, Berlin and Munich, Germany) with a 12-channel phased array head coil. A whole-head, high-resolution T1-weighted, magnetization-prepared rapid gradient-echo (MPRAGE) anatomical volume (acquisition parameters: repetition time [TR] = 2000 ms, echo time [TE] = 3.39 ms, flip angle = 9°, inversion time [TI] = 900 ms, voxel resolution = 1.0 × 1.0 × 1.33 mm, field of view [FOV] = 256 × 256, 128 sagittal slices) was collected prior to the functional runs.

Two functional runs containing 108 volumes each were collected using sparse-sampled T2*-weighted gradient-echo planar imaging (EPI) scans (acquisition parameters: TR = 6000 ms, acquisition time [TA] = 2000 ms, TE = 30 ms, flip angle = 90°, voxel resolution = 3.125 × 3.125 × 4.0 mm, FOV = 200 × 200, and 32 transverse slices acquired parallel to the anterior commissure–posterior commissure [AC-PC] plane, providing whole-brain coverage). Each functional run was preceded by five additional TRs during which no data were recorded to allow for stabilization of longitudinal magnetization. Sparse-sampling (Hall et al., 1999) was used to allow auditory stimuli to be presented in silence, and the sparse-sampling rate (TR = 6 s) was chosen to optimize the trade-off between benefits gained from presenting stimuli in

silence versus fuller and more frequent sampling of the hemodynamic response (Perrachione & Ghosh, 2013).

MRI Data Analysis

Cortical reconstruction and parcellation of anatomical images were performed using the default processing stream FreeSurfer v5.1.0 (Dale, Fischl, & Sereno, 1999).² Functional data were analyzed in SPM8³ using workflows in Nipype v0.4 (Gorgolewski et al., 2011).⁴ Image pre-processing consisted of motion correction (rigid-body realignment to the mean EPI image from the first functional run) and spatial smoothing (6-mm isotropic full width at half-maximum three-dimensional [3-D] Gaussian kernel). Motion and intensity outliers (functional volumes exceeding 1 mm in differential motion or differing from the mean image intensity by > 3 SD) were identified using ART⁵ and regressed out of the hypothesized time series. Model design was implemented using the *modelgen* algorithm in Nipype, and included six task regressors (two-, four-, and six-syllable lengths each for the real-word and nonword conditions), six motion parameters, individual regressors for any outlier volumes, five Legendre polynomial terms to account for low-frequency components of the MR-signal including scanner drift, and a constant term. Vectors for task regressors were determined by convolving a high-temporal-resolution vector of event onsets with their durations, and convolving the resulting stimulation time series with a canonical hemodynamic response function to generate the hypothesized blood oxygenation level dependent response. To account for the discontinuous nature of sparse-sampling MR-signal acquisition, the hypothesized response vector was then resampled over only those time points where MRI data were actually acquired—an approach that offers increased sensitivity to event-related activation in sparse-sampling fMRI by accounting for the neural response sampled across consecutive functional volumes (Perrachione & Ghosh, 2013). Contrasts of interest included each condition versus baseline, real words versus nonwords, each level of each condition individually, and demeaned linear parametric contrasts of the three levels for the real-word and nonword conditions. Within-subject estimation of the general linear model and contrasts was conducted in participants' native EPI space.

The coregistration transformation between each participant's mean functional EPI volume and their T1-weighted structural image was calculated using FreeSurfer's *BBRegister* program with FLIRT initialization (Greve & Fischl, 2009). These transforms were applied to the contrast images from each participant's first-level analysis to ensure accurate coregistration between functional data and high-resolution anatomy. Participants' high-resolution structural images were aligned to a common space (the MNI152 template from

²FreeSurfer: <http://surfer.nmr.mgh.harvard.edu/>

³SPM8: <http://www.fil.ion.ucl.ac.uk/spm/software/spm8/>

⁴Nipype: <http://nipype.org/nipype/>

⁵ART: http://www.nitrc.org/projects/artifact_detect/

FSL v4.1.6⁶ via nonlinear symmetric diffeomorphic mapping implemented in ANTS v1.5 (Avants, Epstein, Grossman, & Gee, 2008).⁷ Each participant's transformation matrix and deformation field from this spatial normalization were applied to their coregistered first-level contrast images to align them to the common space. Second-level group comparisons were performed using SPM8 via Nipype workflows. Following suggestions regarding topological multiple-comparisons correction (Woo, Krishnan, & Wager, 2014), group-level statistics were thresholded voxelwise at a conservative $p < .001$, and correction for multiple comparisons was accomplished by controlling the cluster-level false-discovery rate at $q = .05$.

Anatomical locations of functional group effects were established using the Harvard-Oxford probabilistic atlas provided with FSL. We selected the following core cortical language areas from both cerebral hemispheres to conduct a priori anatomical region-of-interest (ROI) analyses: STG, inferior frontal gyrus (IFG) pars opercularis, IFG pars triangularis, and supplementary motor area (SMA). Anatomical ROIs were determined individually for each participant on the basis of the automatic anatomical parcellation for the Desikan-Killiany brain atlas implemented in FreeSurfer (Desikan et al., 2006; Fischl et al., 2004). Values for anatomical ROI analyses and brain-behavior correlations were extracted from individual participants' coregistered native-space first-level contrast images utilizing *mri_segstats*. The Desikan-Killiany atlas does not contain a parcellation uniquely corresponding to the SMA. To derive the within-subject ROI for the SMA, we applied the inverse transformation from each participant's normalization into common space to the SMA ROI from the Harvard-Oxford atlas. Each resulting native-space image was subsequently masked with the participant's left and right hemisphere cortical ribbon from FreeSurfer using *fslmaths*, providing two within-participant cortical SMA masks. Values for the SMA response across contrasts were extracted using *fslstats*.

Behavioral Data Analysis

Behavioral data were analyzed in R v2.15.2.⁸ Statistics involving repeated measures were conducted using the maximal (generalized) linear mixed-effects model implemented in the lme4 package (Bates, Mächler, & Bolker, 2012). When not returned by the lme4 package, p values for fixed factors were calculated using likelihood ratio tests between the full model and a model excluding the fixed factor of interest (Barr, Levy, Scheepers, & Tily, 2013).

The CNRep is standardized for use with children aged 4–9 years, and contains no standard scores in the age range of participants in the current study. For this reason, only raw scores on the CNRep were used for analysis. The CTOPP is standardized for use with participants up to 25 years. For participants in the present study aged 25–32 years

($N = 8$), CTOPP standard scores were computed from the oldest standardized age bracket (17–24 years; $N = 11$) of this test, consistent with an apparent plateau in performance on this subtest beginning at age 15 years. (The pattern of results obtained by using CTOPP raw scores, or with raw scores controlling for age, did not differ from those obtained using these standard scores).

Results

Neuropsychological Assessments

Results of the neuropsychological assessments for cognitive and language ability are summarized in Table 1. All participants had an average or above-average IQ. All participants also performed in the average or above-average range on the CTOPP phonological awareness composite score (which includes the Elision and Blending Words subtests), with the exception of one participant who scored below average (8th percentile) on the phonological awareness composite (but in the average range of both the CTOPP nonword repetition subtest and the CNRep).

Participants' performance on the tests of nonword repetition was more varied: Five participants scored at or below 1 SD below the age-normed population mean (16th percentile) on the CTOPP Nonword Repetition subtest, and two scored 1 SD above (84th percentile). A similarly wide range of performance was observed on the CNRep.

There was a significant correlation between participants' performance on the CNRep and the CTOPP nonword repetition subtest, $t(14) = 2.75$, $p < .016$, Pearson's $r = .59$. There were no reliable correlations between any of the phonological awareness subtests or their composite and either of the nonword repetition tests, nor was there a relationship between any of the full or partial measures of IQ and performance on the nonword repetition tests.

There was also a significant correlation between participants' performance on the Elision subtest of the CTOPP and their composite IQ, $t(15) = 2.96$, $p = .01$, Pearson's $r = .62$, but not with either of the partial IQ scores individually. No such relationship was seen for the Blending Words subtest, nor the phonological awareness composite score. No relationship was observed between performance on the Elision and Blending Words subtests of the CTOPP.

In-Scanner Behavior

Participants performed with a high degree of accuracy in the scanner in both behavioral conditions (see Table 2). (Technical issues resulted in the loss of in-scanner behavioral data for two participants; $N = 14$ for statistics in this section.) Response accuracy was analyzed with a maximal generalized linear mixed-effects model for binomial data with fixed effects of condition (real words vs. nonwords), phonological working memory load (two, four, or six syllables), and their interaction. The random effects structure of this model consisted of within-participant and within-stimulus intercepts, as well as within-participant slopes for the main effects

⁶FSL: <http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/>

⁷ANTS: <http://picsl.upenn.edu/software/ants/>

⁸R: <http://www.R-project.org>

Table 1. Performance on neuropsychological assessments of phonological working memory and phonological awareness (raw scores).

Test	Subtest	Raw scores			Standard scores		
		<i>M</i>	<i>SD</i>	Sample range	<i>M</i>	<i>SD</i>	Sample range
KBIT-2	Verbal	75.19	3.27	68–80	116.94	6.35	103–127
	Matrices	40.94	3.21	34–46	112.44	7.96	98–126
	Composite	229.38	11.24	209–247	116.44	6.54	105–127
CTOPP	Elision	18.19	3.08	8–20	10.44	2.25	4–12
	Blending	17.38	2.58	9–20	11.56	1.97	6–14
	Phonological awareness composite score	—	—	—	106.00	10.39	79–118
	Nonword repetition	12.88	3.10	7–17	9.31	2.47	5–13
CNRep		35.94	2.57	31–40	—	—	—

Note. The mean, standard deviation, and sample range (minimum–maximum) are listed for both raw and standard scores. For all cells, $N = 16$. KBIT-2 = Kaufman Brief Intelligence Test–Second Edition; CTOPP = Comprehensive Test of Phonological Processing; CNRep = Children’s Test of Nonword Repetition. Standard scores for the CNRep are only available up to age 8 years. Em dash indicates data not available.

and their interaction. Participants performed less accurately with increasing syllable lengths, $z = -3.250$, $p < .0012$.

There was no difference in accuracy between conditions, $z = -0.528$, $p = .60$, and no interaction, $z = 1.213$, $p = .23$.

There was a significant correlation between participants’ in-scanner performance on the nonword discrimination task and their out-of-scanner performance on the Nonword Repetition subtest of the CTOPP ($r = .62$, $p < .018$), but not their out-of-scanner performance on the CNRep ($r = .12$, $p = .69$) despite the strong correlation between these latter two behavioral assessments themselves.

Response times (\log_{10} -transformed to more closely conform to the normal distribution) were also analyzed in a maximal linear mixed-effects model with the same fixed- and random-effects structure as the model of accuracy. Response latency increased with the number of syllables, $t = 10.43$, $p < 2.2 \times 10^{-16}$, but there was no difference in response latency between conditions, $t = -0.05$, $p = 1.0$. There were no reliable relationships between in-scanner behavioral measures and any of the other behavioral assessments.

Whole-Brain Results

In a whole-brain group analysis (see Figure 2a), a number of regions exhibited significant task-related activation to the real-word discrimination condition relative to

rest, including bilateral STG (lateral STG, planum temporale [PT], and Heschl’s gyrus [HG]), bilateral SMA, bilateral ventral precentral gyrus, dorsal left precentral gyrus, left IFG, and right cerebellum. Regions exhibiting task-related deactivations (reduced response to real-word discrimination compared with rest) included clusters in right superior frontal gyrus, right inferior lateral occipital cortex, right inferior temporal cortex, bilateral inferior parietal cortex, bilateral anterior cingulate/medial prefrontal cortex, bilateral pre-cuneus, and bilateral posterior cingulate cortex.

The extent of task-related activation to the nonword discrimination condition relative to rest was similar but more widespread (see Figure 2b), with regions exhibiting significant task-related activation bilaterally, including STG (lateral STG, PT, and HG), SMA, ventral precentral gyrus, lingual gyrus, thalamus, basal ganglia, and cerebellum, as well as left IFG, left dorsal premotor cortex, and left fusiform/inferior temporal cortex. Significant task-related deactivations to the nonword discrimination condition relative to rest were observed in bilateral superior frontal gyrus, medial prefrontal cortex, posterior cingulate, and lateral parietal cortex.

A wide range of regions were significantly more strongly activated by the nonword than real-word discrimination task (see Figure 3), including STG, ventral precentral gyrus, IFG, middle frontal gyrus, SMA, anterior cingulate,

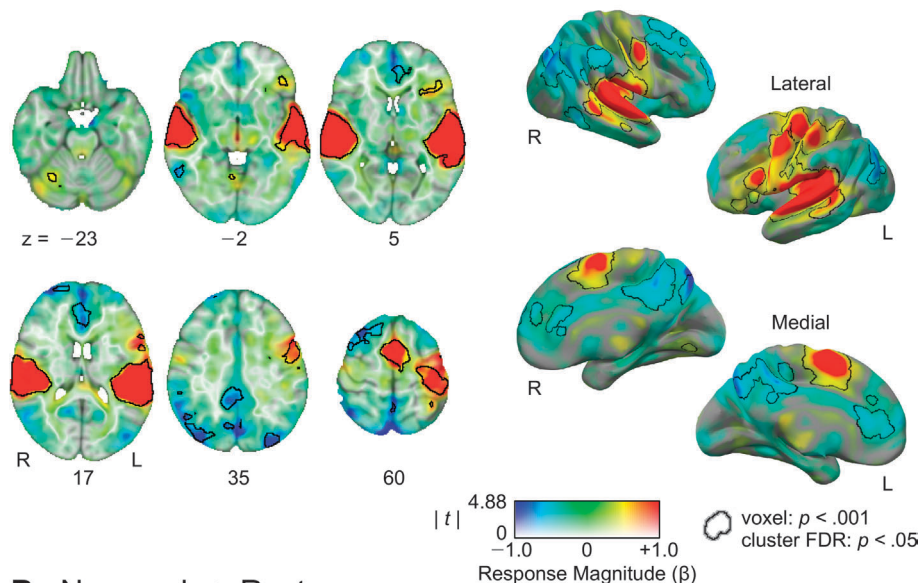
Table 2. In-scanner behavioral performance.

Item	Syllables	Accuracy (%)			Response time (ms)		
		<i>M</i>	<i>SD</i>	Sample range	<i>M</i>	<i>SD</i>	Sample range
Real words	2	91.0	6.46	80.0–100.0	973.39	259.82	556.0–1416.5
	4	92.1	7.47	73.3–100.0	1083.79	296.24	632.0–1714.0
	6	84.0	8.49	66.7–100.0	1189.93	343.83	704.0–1730.0
Nonwords	2	90.5	9.14	63.3–100.0	983.00	223.94	646.5–1337.5
	4	88.8	7.80	70.0–100.0	1114.93	257.25	763.5–1582.0
	6	77.1	13.73	51.7–93.0	1294.04	231.13	956.0–1643.0

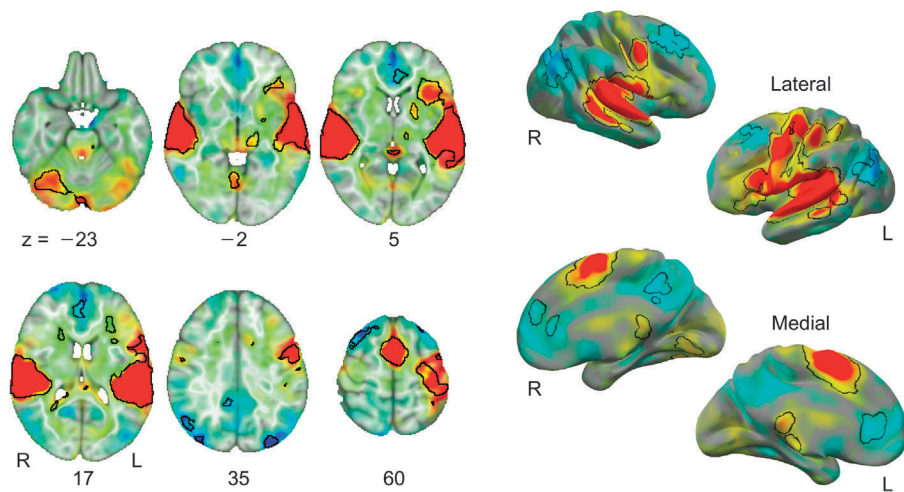
Note. The mean, standard deviation, and sample range (minimum–maximum) of participants’ in-scanner accuracy and response times in each syllable level of each condition are listed. For all cells, $N = 14$.

Figure 2. Task-related brain response versus baseline. Performance of real-word (A) and nonword (B) discrimination tasks elicited significant activation throughout the brain, including perisylvian cortices, lateral and medial motor cortices, thalamus, and cerebellum. Brain areas associated with the default-mode network showed reduced response magnitude during the task. Color scale denotes the magnitude of the group average response; warm colors indicate increased activation relative to baseline (rest); cool colors indicate reduced activation. Color opacity increases with increasing voxelwise significance of the effect, $t(15) \geq 4.88$, $p < .0001$, fully opaque. Areas of statistically significant physiological response ($p < .001$, cluster-level false-discovery rate correction $q < .05$) are outlined in black. Response-magnitude maps are overlaid on axial slices (left) or partially inflated surfaces (right) of the MNI152 template brain for anatomical localization. Axial slices are displayed in radiological convention; z indicates location in MNI space. FDR = false-discovery rate.

A. Real words > Rest



B. Nonwords > Rest



inferior temporal gyrus, fusiform gyrus, precuneus, cuneus, insula, basal ganglia, thalamus, and cerebellum (all bilaterally). There were no clusters in which greater response was elicited during the discrimination of real words than nonwords.

Parametric Effects of Phonological Working Memory Load

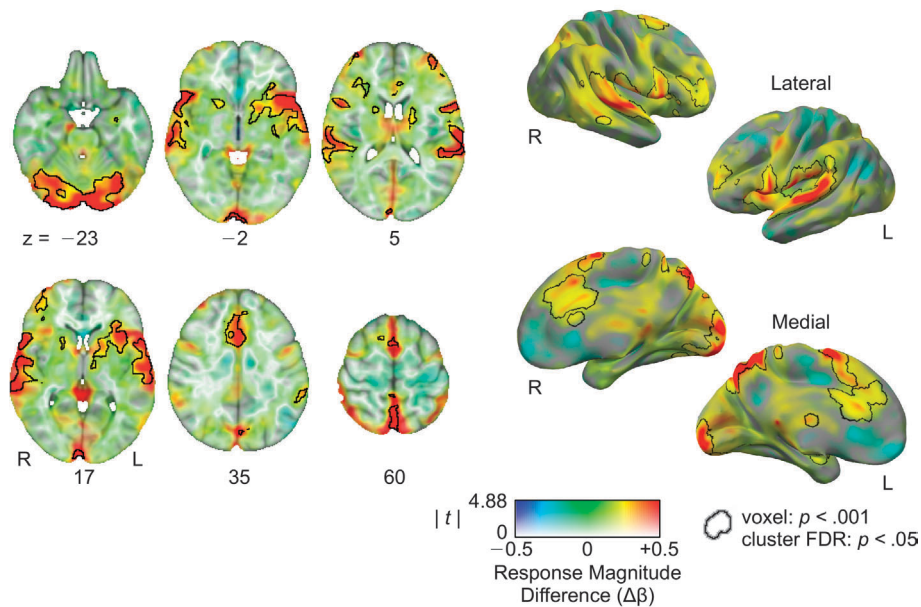
In the real-word discrimination condition, significant parametric effects of increasing word length on

physiological response were only observed in bilateral STG (including lateral STG, PT, and HG) and cortex on the dorsal face of the Sylvian fissure. Significant parametric effects in the nonword discrimination condition (see Figure 4b) were observed more widely, including bilateral STG (lateral, PT, and HG), bilateral middle temporal gyrus, bilateral SMA, and left IFG.

To investigate how the properties of these parametric effects varied across regions and conditions, we performed anatomically constrained ROI analyses on the basis of four

Figure 3. Greater physiological response when discriminating nonwords versus real words. Activation related to the nonword discrimination task was of significantly greater magnitude than that related to real-word discrimination in many brain areas, including superior temporal gyrus, inferior frontal gyrus (IFG), insula, (pre-)supplementary motor area (SMA), anterior cingulate, basal ganglia, and cerebellum. Some areas of difference (e.g., superior parietal lobe) reflect reduced deactivation for nonwords compared with real words (see Figure 2). All figure conventions as in Figure 2. FDR = false-discovery rate.

Nonwords > Real words



cortical areas known a priori to comprise core parts of the spoken language processing system (see Figure 5). Mean functional activation in each ROI was analyzed in a repeated-measures analysis of variance in R using the *ez* package (Lawrence, 2012) with condition (real words vs. nonwords), phonological working memory load (two, four, or six syllables), and hemisphere (left or right) as within-participant factors.

In all four cortical areas, the ROI analyses replicated both the main effects of condition (greater response during nonword discrimination) and parametric effect of phonological working memory load (greater response with increasing number of syllables) observed in the whole-brain analyses. The ROI analyses further revealed the following additional effects: In STG, a significant interaction between condition and phonological working memory load was observed, $F(1, 15) = 12.18, p < .0033, \eta^2 = .083$, such that increasing the number of syllables resulted in a greater increase in activation for nonwords than for real words. No hemispheric differences were observed in STG. In IFG, larger overall responses tended to be observed in the left hemisphere than in the right (pars opercularis: $F[1, 15] = 16.40, p < .0011, \eta^2 = .420$; pars triangularis: $F[1, 15] = 12.70, p < .003, \eta^2 = .303$)—an effect not influenced by condition or phonological working memory load. In the SMA, a significant interaction between condition and phonological working memory load was observed, $F(1, 15) = 13.16, p < .0025, \eta^2 = .118$, such that increasing the number of syllables again resulted in a greater increase in activation for nonwords

than for real words. Similar to IFG, the SMA also tended to respond more strongly in the left hemisphere than the right, $F(1, 15) = 32.18, p < .00005, \eta^2 = .304$; additionally, the parametric effect of increasing working memory load was stronger in the left hemisphere than the right, $F(1, 15) = 4.70, p < .05, \eta^2 = .003$, although the magnitude of this difference was small.

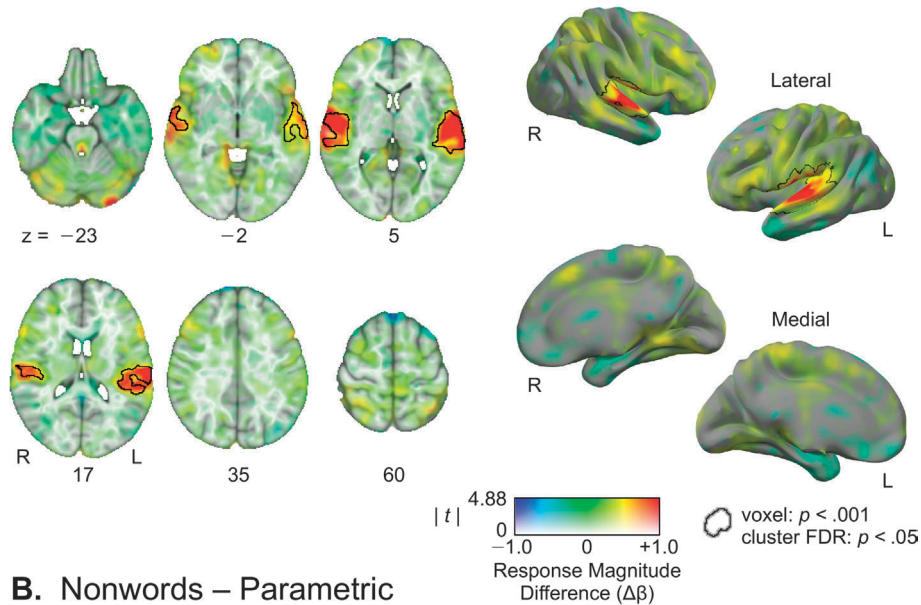
Brain and Behavior Correlations

Participants' performance on the CNRep clinical assessment was significantly associated with the magnitude of their physiological response in left STG to the nonword discrimination task (contrast: All Nonwords > Rest; see Figure 6), $t(14) = 3.37, p < .005$, Pearson's $r = .67$. A similar effect was observed in the right STG, $t(14) = 2.28, p < .04$, Pearson's $r = .52$. These relationships did not change when age was included as a covariate (because CNRep standard scores are not available for our age range). No such correlations were observed in any of the other anatomical ROIs, and no significant brain-behavior correlations were observed for nonword repetition performance on the CTOPP.

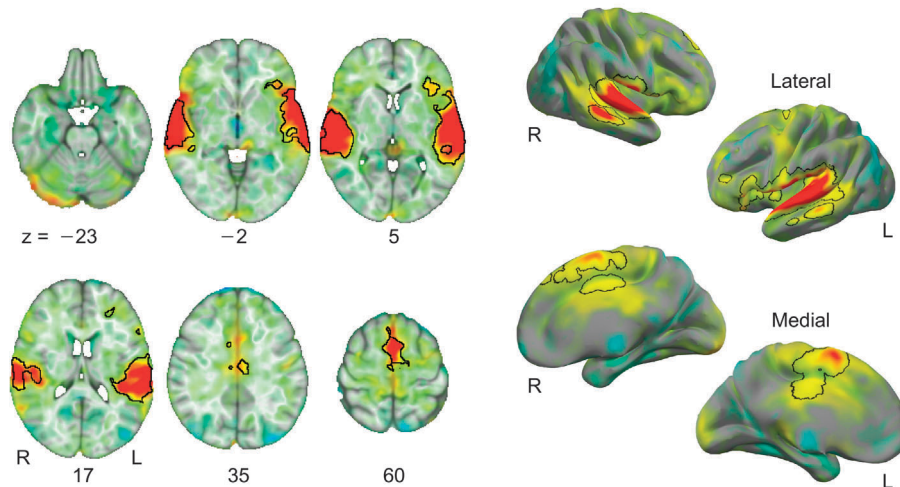
We tested the predictive generalizability of the relationship between STG activation and phonological working memory ability with a conservative leave-one-out cross-validation approach. Linear models of the relationship between these two factors were computed for all permutations of $N - 1$ participants, and these models were used to

Figure 4. Parametric modulation of brain response with increasing phonological working memory load. For real words (A), increasing activation with increasing phonological working memory load was seen exclusively in superior temporal gyrus. For nonwords (B), the parametric response was greater in magnitude and more widespread, including superior temporal, inferior frontal, and supplementary motor areas. All figure conventions as in Figure 2. FDR = false-discovery rate.

A. Real words – Parametric



B. Nonwords – Parametric



predict the CNRep score for the independent N th participant. This approach produced reliable predictions of actual CNRep scores when using activation measured in left STG ($R^2 = .27$), but not when using activation measured in right STG ($R^2 = .06$).

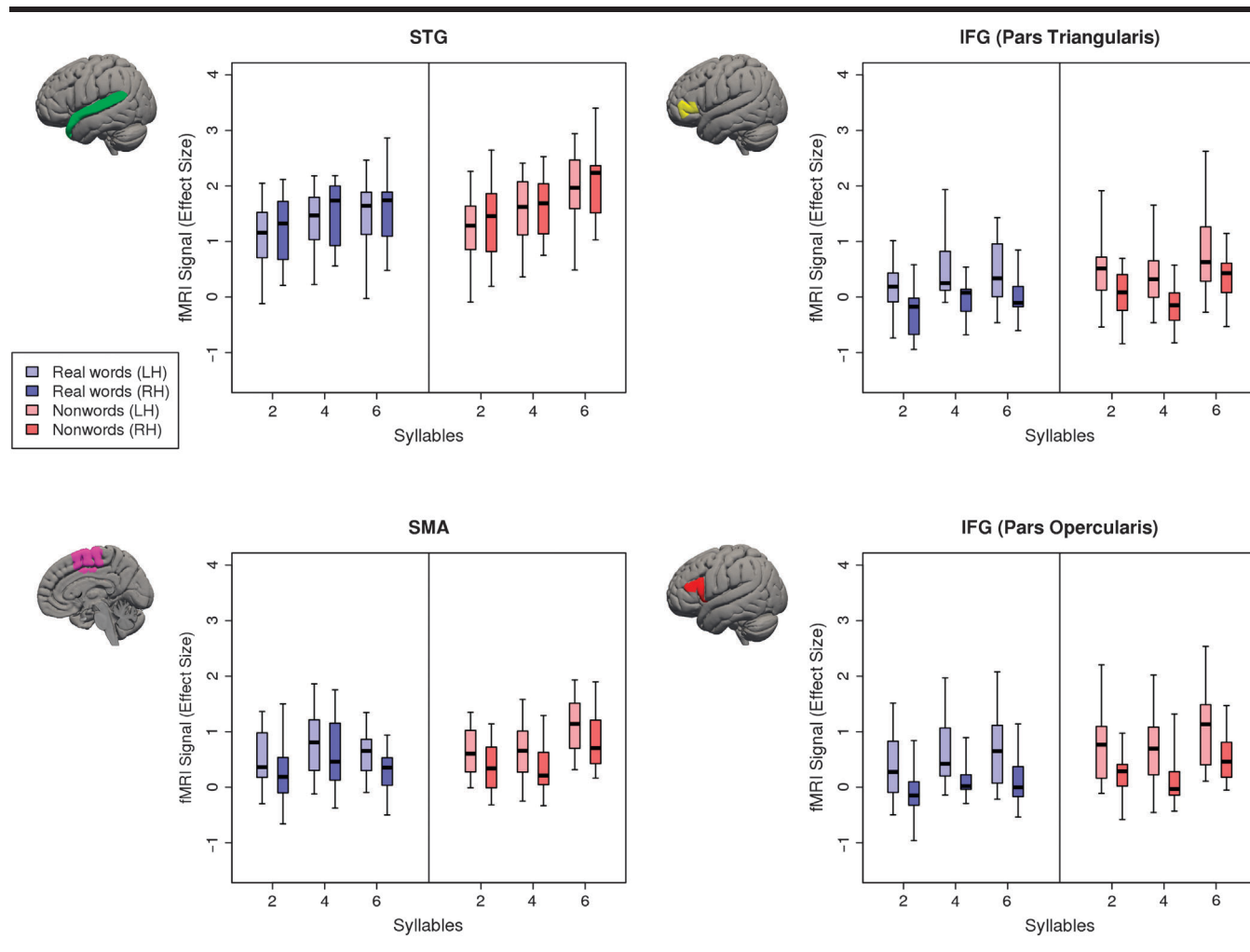
Discussion

In this study, we examined the whole-brain neural response to auditorily presented real-word and nonword stimuli in a discrimination paradigm in which phonological working memory load was manipulated by parametrically varying the number of syllables. In terms of behavior, a

greater number of syllables was associated with less accurate and slower performance for both words and nonwords, indicating that stimuli with more syllables placed an increasing demand on phonological working memory. Compared with rest, cortical response to auditory real words was confined to perisylvian cortex bilaterally, predominately in the superior temporal lobe, left IFG, and SMA. The response to nonwords was stronger in magnitude and more distributed throughout both cortical and subcortical areas, although perisylvian cortices and the SMA remained the areas of strongest response.

We sought to identify the areas contributing to phonological working memory under the hypothesis that the

Figure 5. Parametric activation in select anatomical regions of interest. Whole-brain analysis revealed linearly increasing activation of bilateral superior temporal gyrus (STG), inferior frontal gyrus (IFG), and supplementary motor area (SMA) with increasing phonological working memory load. The nature of this effect across anatomical regions of interest (ROIs) is illustrated here—for statistics and full description of these effects, see main text. Boxplots: Solid, dark horizontal line indicates condition median; filled areas encode middle 50%; whiskers extend to maximum and minimum values. Left panels display response to real-word conditions; right panels, nonwords. Lighter shading indicates left hemisphere (LH) values; darker shading, right hemisphere (RH). ROI locations are illustrated on cortical surfaces at left. fMRI = functional magnetic resonance imaging.



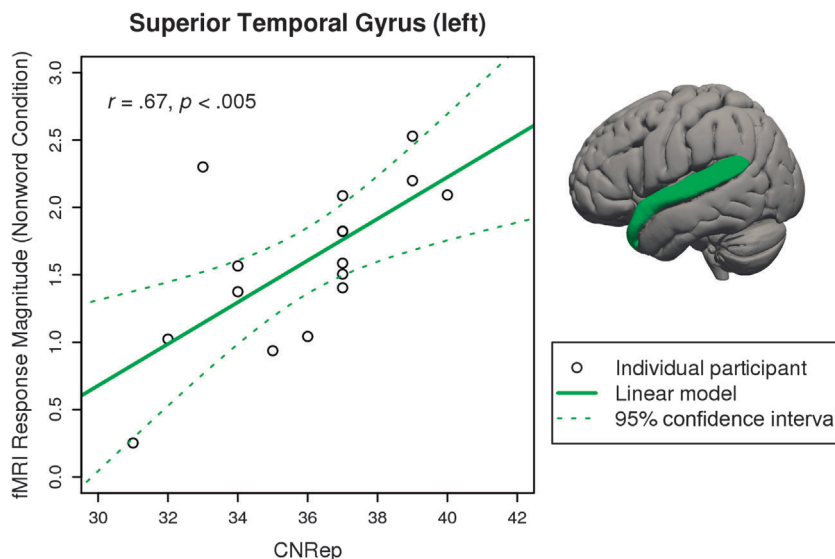
regions supporting this ability would exhibit a scaling physiological response with increasing phonological working memory load (Braver et al., 1997). We therefore parametrically manipulated phonological working memory load by increasing the number of syllables in the stimuli, because nonwords with more syllables are known to result in more repetition errors than shorter nonwords (e.g., Gathercole et al., 1994). Such scaling responses were observed principally in bilateral STG for both real words and nonwords, and additionally in bilateral SMA and left IFG for nonwords.

The identification of STG, SMA, and IFG as a network for phonological working memory is in line with prior observations of Strand et al. (2008). In that study, variable-length nonwords were used in a delayed match-to-sample task to probe to the cerebral foci of processes related to encoding, storage, and retrieval of auditory information

during phonological working memory. Strand et al. reported significant response in IFG and SMA during the encoding of a target nonword stimulus, in all three regions (STG, SMA, and IFG) during a long maintenance delay, and in IFG and SMA at the time of participant response.

The present study provides a number of important extensions to Strand et al.'s (2008) observations. First, we used an immediate response paradigm with highly word-like nonword stimuli, consistent with the design of most clinical nonword repetition assessments, whereas Strand et al. used a compulsory response delay for rehearsal. This provides additional evidence that the regions identified here and by Strand et al. are relevant to clinically sensitive nonword repetition measures involving immediate responses, as opposed to arising only from long rehearsal delays. Second, we observed robust scaling in physiological response

Figure 6. Correlation between neural response to auditory nonword stimuli and performance on the Children’s Test of Nonword Repetition (CNRep). Higher performance on the CNRep assessment was significantly and reliably associated with greater physiological response during the nonword discrimination task in left superior temporal gyrus. fMRI = functional magnetic resonance imaging.



in these regions to parametric manipulation of phonological working memory load. Although Strand et al. also used a syllable length-based load manipulation, they reported finding no parametric effects. This difference may be due to the longer (five- to nine-syllable) nonwords used in that study, because working memory demands near capacity can have nonlinear effects on load-based response in fMRI (reviewed in Linden, 2007). Third, our choice to use sparse-sampling fMRI acquisition makes the present study more sensitive to the role of the STG in phonological working memory than the continuous-sampling approach taken previously. This increased sensitivity may reflect the more substantial and extensive activation we observe in STG compared with the study by Strand et al.—a result that may also be due in part to different baseline conditions between the present study (rest) and that of Strand et al. (passive listening).

Furthermore, although Strand et al. (2008) did not report a brain-behavior relationship, we observed a robust and reliable relationship between neural response in left STG to nonwords and participants’ nonword repetition ability as measured out of the MRI scanner by the CNRep—a standardized clinical assessment of phonological working memory. This relationship further implicates left STG as a core phonological working memory area, beyond its maintenance role identified by Strand et al. Taken together with the results of Strand et al., the present results indicate that STG, IFG, and SMA together constitute the developmentally mature cortical network underlying performance on these canonical, clinically relevant phonological working memory tasks (see also Markiewicz & Bohland, 2016). Future studies will therefore be able to use this network as a foundation for understanding how the neural systems for

phonological working memory change during development and the ways in which they may differ in developmental communication disorders.

The STG and Models of Phonological Working Memory

A widely acknowledged contemporary model of phonological working memory holds that verbal information is actively maintained in short-term memory through the interaction of a phonological buffer with articulatory rehearsal processes (Baddeley, 1992, 2003). This model explicitly conceptualizes the phonological buffer as a distinct cognitive module independent of core linguistic processes such as auditory perception and phonological encoding. An alternate, emerging view, derived from a synthesis of behavioral (Acheson & MacDonald, 2009) and neuroimaging (Hickok, 2009) research holds that, instead of a phonological buffer divorced from core language systems, processing and storage for phonological working memory are subserved by canonical systems for speech perception and production (Jacquemot & Scott, 2006; Majerus, 2013; Postle, 2006).

Support for these latter models, in which the phonological encoding and storage are integrated, comes from accumulating evidence about the convergent role of STG in both speech perception and phonological working memory. The superior temporal regions implicated in studies of phonological working memory, including the present study, appear to be largely the same as those identified by other studies of speech and language as supporting core phonological processing (e.g., Graves, Grabowski, Mehta, & Gupta, 2008; McGettigan et al., 2011; Peeva et al., 2010;

Wilson, Isenberg, & Hickok, 2009). The observation that regions responsible for phonological encoding during speech perception also subserve storage of verbal information during working memory tasks favors integrative models of phonological working memory, such as those of Jacquemot and Scott (2006) and Majerus (2013). To be specific, if a synergy between posterior perceptual regions responsible for phonological encoding and anterior regions responsible for articulatory planning is sufficient to store, update, and maintain short-term traces of verbal information (Hickok, 2009; Postle, 2006; Ruchkin et al., 2003), this obviates the need for a dedicated, independent buffer module (Baddeley, 1992, 2003) that is instantiated elsewhere in “domain-general” cortex such as inferior parietal lobe or dorsolateral prefrontal cortex (Jonides et al., 1998; Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000; E. E. Smith, Jonides, Marshuetz, & Koeppe, 1998). Therefore, there is an increasingly sophisticated behavioral literature demonstrating that the sequencing and short-term maintenance of verbal information is influenced by core linguistic (Schweppe & Rummer, 2007), phonological (Jones, Hughes, & Macken, 2006; Page, Madge, Cumming, & Norris, 2007; Rispens & Baker, 2012), and even auditory (Jones & Macken, 1993) and articulatory (Keren-Portnoy, Vihman, DePaolis, Whitaker, & Williams, 2010) processing mechanisms.

The present study provides additional evidence to favor the interpretation of left STG as a core phonological working memory area, and therefore of integrative models of phonological memory and speech perception. First, left STG exhibited greater responses to nonwords than to real words (see Figure 3), consistent with the increased working memory demands of that condition (see Table 2). Second, left STG exhibited a scaling physiological response corresponding to the increasing storage demands of longer nonwords (see Figure 4). Third, greater response magnitude in this region during the nonword discrimination task was significantly correlated with better behavioral performance on an established clinical test of nonword repetition (see Figure 5). These results were obtained in a sample drawn from the population at large, rather than one selected for a particular deficit such as SLI or dyslexia, indicating that the functional properties of this region are related to even nonclinical variation in phonological working memory ability. Because these results were obtained in a population of control adults with typical developmental profiles, they will be able to serve as a normative baseline for interpreting the results of future studies investigating the development of these neural systems in children, as well as how they may differ in individuals with developmental communication disorders.

However, caution must be exercised to avoid concluding that the colocalization of phonological working memory and speech perception in the posterior superior temporal lobe necessarily means that these two behaviors depend on common computational processes. The functional neuroanatomy of the brain is highly dynamic, and even a narrowly circumscribed area can support multiple unique functions. The same or proximal areas that we have

identified in the present study as being sensitive to phonological working memory load have also been assigned a variety of other functions depending on the nature of the in-scanner task (Griffiths & Warren, 2002; Hein & Knight, 2008; Price, Thierry, & Griffiths, 2005). Future work will need to draw on more sensitive analyses (e.g., Markiewicz & Bohland, 2016; Peelen & Downing, 2006) to determine the extent to which the colocalization we and others have observed reflects the common computational processes suggested by a growing behavioral literature in psycholinguistics.

A full model of verbal working memory will need to harmonize the growing evidence for the role of language areas in phonological working memory (e.g., Buchsbaum & D’Esposito, 2008; Majerus, 2013; Strand et al., 2008) with the earlier literature implicating domain-general frontal and parietal regions in working memory (e.g., Braver et al., 1997; Paulesu et al., 1993; E. E. Smith et al., 1996). Sophisticated neuroimaging studies drawing on the tradition of working memory tasks from cognitive psychology have shown that these regions respond in a load-dependent manner to both auditory and visual stimuli (e.g., Cowan et al., 2011). Whether such activation in these frontal and parietal regions reflects the executive demands of working memory tasks that involve executive manipulation or selection, such as in the Sternberg task (e.g., Barde & Thompson-Schill, 2002), whether they are brought online as a function of the rehearsal demands of the retention delay (cf. Strand et al., 2008), or whether there is something particularly “linguistic” about nonword repetition tasks that preferentially recruits areas associated with speech perception and production (e.g., Hope et al., 2014; Yoo et al., 2012) remains an open and important avenue for future research.

The present results, however, lend support to integrative models of phonological working memory, in which STG plays a central role in both processing and short-term storage of phonological material. Our observations that activation of this region both scales parametrically with increasing working memory load and correlates with individual differences in nonword repetition abilities highlights this region as potentially playing an important role in the sorts of phonological working memory tasks on which children and adults with developmental communication disorders show deficits. A more sophisticated understanding of neural function may therefore not only favor one cognitive theory (i.e., integrated models of phonological working memory) over another. It may also help us refine our conceptualization of phonological working memory impairments in developmental communication disorders—not as deficits in domain-general memory processes, but rather in phonological processing and representation in particular. Whether and how the working memory functions of superior temporal region are disrupted in developmental communication disorders must become a principal goal of future work in this domain. Therefore, such research may also aid in determining how phonological working memory and phonological processing and representations support one another in development (Acheson & MacDonald, 2009; Hickok, 2009; Melby-Lervåg et al., 2012; cf. Gathercole

& Baddeley, 1993) and how to capitalize on these relationships in the accurate identification and remediation of developmental communication disorders.

Working Memory Load and the Structure of Nonwords

There was a correlation between one clinical test of phonological working memory (the CNRep) and physiological response in the STG region, but no significant correlation was observed for the other test (CTOPP) despite participants' performance on these two measures themselves being highly correlated and performance on the latter being correlated with their in-scanner nonword discrimination accuracy. This difference may have arisen due to fundamental differences in the design of the nonword stimuli in the CTOPP, CNRep, and present experiment. In both the CNRep and present experiment, the nonword stimuli are highly wordlike, such that their phonotactic probabilities are much more similar to those of real words (and not different from the representative set of real words used in the present experiment), whereas the nonwords used in the CTOPP are less like real English words and have comparatively low phonotactic probability. Nonwords vary with respect to their internal complexity and wordlikeness (see Graf Estes et al., 2007, for a review). In this way, their encoding and repetition is susceptible to the effects of long-term linguistic experience (e.g., Archibald, Gathercole, & Joanisse, 2009; Frisch, Large, & Pisoni, 2000; Gathercole, 1995; Gathercole, 2006; Keren-Portnoy et al., 2010; Metsala & Chisholm, 2010; Munson, 2006; B. Smith, 2006; Vitevich, 2006), revealing the complex relationship between language development, phonological working memory, and the nonword repetition tests that assess it. In typical development, the less wordlike nonwords are, the more difficult they are to repeat, suggesting that listeners draw on their long-term experience with the statistical properties of language to facilitate nonword repetition (Melby-Lervåg et al., 2012). These factors correspondingly bear on nonword repetition by individuals with developmental disorders of language in complex ways: Although some behavioral studies investigating the effects of wordlikeness on nonword repetition abilities by individuals with SLI have suggested similar (Briscoe, Bishop, & Norbury, 2001) or even greater (Munson, Kurtz, & Windsor, 2005) effects of this factor, others have speculated that the nature of language impairments may reduce the importance of this factor (Archibald & Gathercole, 2006). Last, although there exists a small literature investigating the effects of phonotactic probability or wordlikeness on brain response to words and nonwords (Majerus et al., 2002; Papoutsis et al., 2009; Raettig & Kotz, 2008; Vaden et al., 2011), it remains to be shown whether and how the response of the speech processing network is influenced by an interaction between long-term knowledge of the statistical properties of word structure and phonological working memory load.

Although we operationalized phonological working memory load by the number of syllables in the word and nonword stimuli, we are not claiming that the syllable is

the basic unit of phonological working memory storage. Extensive work has considered the question of working memory capacity and the various units (syllables, words, locations, etc.) that might index working memory load. Indeed, short-term storage of information is facilitated by “chunking” processes, in which working memory demands can be streamlined on the basis of the stimuli's relationship to material in long-term memory (e.g., Cowan, 2000). In any case, as our stimuli increased in number of syllables, they also increased in number of phonemes (nonwords: $r = .95$; real words: $r = .94$), apparent morphological decomposition (nonwords: $r = .69$; real words: $r = .78$), and simple duration of acoustic stimulation (nonwords: $r = .94$; real words: $r = .90$). Thus, using these stimuli, the particular parametrization of working memory load is unlikely to affect the pattern of activation results observed. However, the issue of chunking does highlight an important distinction between the nonword and real-word conditions in this experiment: All of the real word stimuli can potentially be reduced to a single chunk—the word itself—whereas chunking processes will be less effective at reducing the working memory demands of the nonword stimuli, leaving the listener with a larger amount of material to maintain in working memory. This distinction may account for some of the differences in magnitude and extent of the brain responses seen between the real-word and nonword conditions (see Figures 3 and 4). On the other hand, these differences may be due to the degree of similarity between nonword versus real-word pairs: Nonword pairs differed minimally, making detection of these differences more challenging compared with real words, for which minimal pairs are uncommon or nonexistent at longer syllable lengths.

Phonological Working Memory Beyond Left STG

In addition to sensory and association areas of the STG, these results implicate two prefrontal motor planning areas in a phonological working memory network: the IFG and SMA. Both regions are established contributors to speech production (Bohland & Guenther, 2006; Brendel et al., 2010; MacNeilage, 2008; Peeva et al., 2010; Penfield & Welch, 1951) but are nonetheless observed during purely receptive phonological working memory tasks (e.g., Awh et al., 1996; Rauschecker, Pringle, & Watkins, 2008; Strand et al., 2008). Both of these regions exhibited scaling response with increasing phonological working memory load in the present study as well, despite the purely receptive nature of the phonological working memory task. This suggests these regions play an active role in processes underlying phonological working memory, most likely those canonically described as “articulatory rehearsal” (Baddeley, 2003; Hickok, 2009; Jacquemot & Scott, 2006). This may be especially true for the SMA, where parametric response was observed principally for the nonword stimuli, for which no long-term lexical representations were available to support the demands of the working memory task (see also Hartwigsen et al., 2013). The consistent implication of the SMA in both expressive language tasks of polysyllabic speech production

and receptive language tasks of phonological working memory make a strong case for its explicit inclusion in models of speech processing (MacNeilage, 2008; cf. Hickok, Houde, & Rong, 2011; Hickok & Poeppel, 2007).

In addition to increasing demands on phonological working memory, both word and nonword stimuli with more syllables also necessarily involved auditory (acoustic) stimulation for greater durations. However, the scaling responses observed in STG, IFG, and SMA are unlikely to simply reflect acoustic duration for three reasons: First, there was a clear behavioral effect of increasing syllable load (see Table 2). Second, prior research has shown that merely increasing the duration of auditory stimulation has negligible effects on the magnitude or extent of auditory cortical activation (Jäncke et al., 1999). Third, areas with physiological responses that scaled significantly with increasing number of syllables included not only auditory sensory and association areas, but also nonauditory frontal areas responsible for motor planning and core language (IFG, SMA, and ventral precentral gyrus; see Figures 4 and 5).

Beyond the core STG, IFG, and SMA network observed for increasing phonological working memory load, the nonword discrimination task overall recruited a number of other brain areas known to be involved in the perception and production of speech, including dorsal motor cortex, left thalamus, and right cerebellum. Moreover, recruitment of these areas was greater during discrimination of nonwords than real words. What role might these regions play in nonword discrimination that is not explained by phonological working memory load? Dorsal motor cortex activation, observed in only the left hemisphere, is likely related to finger movement for button press during the manual same/different response. Cerebellar activation during speech production has been found to vary in a stepwise fashion, coming online when the demands of speech production are challenging but not showing a linear response with increasing demands (Ackermann, 2008; Wildgruber, Ackermann, & Grodd, 2001). It may therefore be the case that a tonic level of activation in this region is associated with nonword discrimination—a cognitively challenging task, particularly compared with real word discrimination. Because the cerebellum was always “on,” its response did not scale with increasing task demands, and therefore it was not identified by the parametric model.

A final point of consideration is whether phonological working memory, appearing mainly supported by perisylvian cortex, is also primarily supported by left-lateralized language areas, as opposed to being subserved by the auditory system bilaterally. Data from fMRI are frequently equivocal with respect to lateralization, and the task-based (see Figure 2) and parametric (see Figure 4) results in the present study are no exception. Even the contrast between words and nonwords did not reveal any overwhelmingly lateralized differences between these conditions (see Figure 3). Although phonological working memory may take advantage of bilateral, presumably homologous cortical areas in the healthy, intact brain, there are reasons to believe that phonological working memory critically relies on the left hemisphere

in particular. TMS studies of phonological working memory have shown that disruption of the posterior superior temporal region in the left hemisphere disrupts phonological working memory as well as language production (Acheson et al., 2011); however, corresponding sites in the right hemisphere were not assessed. Lesion studies, on the other hand, have overwhelmingly demonstrated that phonological working memory deficits are associated with specifically left hemisphere injury (e.g., Koenigs et al., 2011; Leff et al., 2009). Structural neuroimaging studies have also found relationships between superior temporal morphology of the left, but not right, hemisphere and phonological working memory ability (Richardson et al., 2011). In the results of the present study, there were several plausible indications of a dominant left hemisphere role in phonological working memory: (a) Task-evoked response was greater in both left IFG and left SMA than their right homologues, (b) the effect of the parametric manipulation was stronger in left than right SMA, and (c) the correlation between activation in the nonword condition and behavioral performance on the CNRep was more reliable in the left STG than right. No evidence of rightward asymmetry was observed on any measure. Taken together with the causal findings from lesion and TMS research, these correlational results support a view in which phonological working memory is supported by a distinct set of homologous bilateral cortical areas but is critically dependent on a left-lateralized network of core language areas.

Conclusions

The present results delineate a cortical network consisting of three core areas—STG, IFG, and SMA—that support phonological working memory in tasks analogous to clinical assessments of nonword repetition. These areas are implicated in phonological working memory in the present study through both their scaling response with increasing phonological working memory load (as parameterized by increasing nonword length) and their relationship to behavioral measures of phonological working memory capacity. This network of brain areas closely parallels those previously shown to support core phonological processing, consistent with (but not causally demonstrative of) models of phonological working memory as an emergent property of the language system. Moreover, these results provide a framework for investigating the brain bases of phonological working memory deficits in developmental communication disorders, such as SLI, dyslexia, autism, and Down syndrome—suggesting that nonword repetition impairments are likely to arise from dysfunction of core language areas rather than areas supporting domain-general cognition.

Acknowledgments

Research in this report was supported by the Ellison Medical Foundation and by the National Institute on Deafness and Other Communication Disorders under Grant R01DC011339 to J.G. T.P. was supported in part by a National Science Foundation

Graduate Research Fellowship and by National Institute on Deafness and Other Communication Disorders Grant R03DC014045. The content is solely the responsibility of the authors and does not necessarily represent the official views of the National Institutes of Health. We thank Patricia Saxler, John Lymberis, Elizabeth Norton, Sonia Cosman, Cindy Gibbs, Sheeba Arnold, Steve Shannon, and Christina Triantafyllou. Imaging was performed at the Athinoula A. Martinos Imaging Center at McGovern Institute for Brain Research, Massachusetts Institute of Technology.

References

- Acheson, D. J., Hamidi, M., Binder, J. R., & Postle, B. R. (2011). A common neural substrate for language production and verbal working memory. *Journal of Cognitive Neuroscience*, *23*, 1358–1367.
- Acheson, D. J., & MacDonald, M. C. (2009). Verbal working memory and language production: Common approaches to the serial ordering of verbal information. *Psychological Bulletin*, *135*, 50–68.
- Ackermann, H. (2008). Cerebellar contributions to speech production and speech perception: Psycholinguistic and neurobiological perspectives. *Trends in Neurosciences*, *31*, 265–272.
- Adams, A. M., & Gathercole, S. E. (1995). Phonological working-memory and speech production in preschool-children. *Journal of Speech and Hearing Research*, *38*, 403–414.
- Adams, A. M., & Gathercole, S. E. (1996). Phonological working memory and spoken language development in young children. *Quarterly Journal of Experimental Psychology Section A: Human Experimental Psychology*, *49*, 216–233.
- Anderson, J. D., Wagovich, S. A., & Hall, N. E. (2006). Nonword repetition skills in young children who do and do not stutter. *Journal of Fluency Disorders*, *31*, 177–199.
- Archibald, L. M. D., & Gathercole, S. E. (2006). Nonword repetition: A comparison of tests. *Journal of Speech, Language, and Hearing Research*, *49*, 970–983.
- Archibald, L. M. D., Gathercole, S. E., & Joanisse, M. F. (2009). Multisyllabic nonwords: More than a string of syllables. *The Journal of the Acoustical Society of America*, *125*, 1712–1722.
- Avants, B. B., Epstein, C. L., Grossman, M., & Gee, J. C. (2008). Symmetric diffeomorphic image registration with cross-correlation: Evaluating automated labeling of elderly and neurodegenerative brain. *Medical Image Analysis*, *12*, 26–41.
- Awh, E., Jonides, J., Smith, E. E., Schumacher, E. H., Koeppel, R. A., & Katz, S. (1996). Dissociation of storage and rehearsal in verbal working memory: Evidence from Positron Emission Tomography. *Psychological Science*, *7*, 25–31.
- Baddeley, A. (1992). Working memory. *Science*, *255*, 556–559.
- Baddeley, A. (2003). Working memory: Looking back and looking forward. *Nature Reviews Neuroscience*, *4*, 829–839.
- Baddeley, A., Gathercole, S., & Papagno, C. (1998). The phonological loop as a language learning device. *Psychological Review*, *105*, 158–173.
- Barde, L. H. F., & Thompson-Schill, S. L. (2002). Models of functional organization of the lateral prefrontal cortex in verbal working memory: Evidence in favor of the process model. *Journal of Cognitive Neuroscience*, *14*, 1054–1063.
- Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, *68*, 255–278.
- Barry, J. G., Hardiman, M. J., & Bishop, D. V. M. (2009). Mismatch response to polysyllabic nonwords: A neurophysiological signature of language learning capacity. *PLoS One*, *4*, e6270.
- Bates, D., Mächler, M., & Bolker, B. (2012). lme4: Linear mixed-effects models using eigen and jags. R package version 0.999999-0. Available at <http://CRAN.R-project.org/package=lme4>
- Boersma, P. (2001). Praat, a system for doing phonetics by computer. *Glott International*, *5*, 341–345.
- Bohland, J. W., & Guenther, F. H. (2006). An fMRI investigation of syllable sequence production. *NeuroImage*, *32*, 821–841.
- Braver, T. S., Cohen, J. D., Nystrom, L. E., Jonides, J., Smith, E. E., & Noll, D. C. (1997). A parametric study of prefrontal cortex involvement in human working memory. *NeuroImage*, *5*, 49–62.
- Brendel, B., Hertrich, I., Erb, M., Lindner, A., Riecker, A., Grodd, W., & Ackermann, H. (2010). The contribution of mesiofrontal cortex to the preparation and execution of repetitive syllable production: An fMRI study. *NeuroImage*, *50*, 1219–1230.
- Briscoe, J., Bishop, D. V. M., & Norbury, C. F. (2001). Phonological processing, language, and literacy: A comparison of children with mild-to-moderate sensorineural hearing loss and those with specific language impairment. *Journal of Child Psychology and Psychiatry and Allied Disciplines*, *42*, 329–340.
- Buchsbaum, B. R., & D'Esposito, M. (2008). The search for the phonological store: From loop to convolution. *Journal of Cognitive Neuroscience*, *20*, 762–778.
- Buchsbaum, B. R., Olsen, R. K., Koch, P., & Berman, K. F. (2005). Human dorsal and ventral auditory streams subserve rehearsal-based and echoic processes during verbal working memory. *Neuron*, *48*, 687–697.
- Byrd, C. T., McGill, M., & Usler, E. (2015). Nonword repetition and phoneme elision in adults who do and do not stutter: Vocal versus nonvocal performance differences. *Journal of Fluency Disorders*, *44*, 17–31.
- Byrd, C. T., Vallery, M., Anderson, J. D., & Sussman, H. (2012). Nonword repetition and phoneme elision in adults who do and do not stutter. *Journal of Fluency Disorders*, *37*, 188–201.
- Clark, N. B., McRoberts, G. W., Van Dyke, J. A., Shankweiler, D. P., & Braze, D. (2012). Immediate memory for pseudo-words and phonological awareness are associated in adults and pre-reading children. *Clinical Linguistics & Phonetics*, *26*, 577–596.
- Conti-Ramsden, G., Botting, N., & Faragher, B. (2001). Psycholinguistic markers for specific language impairment (SLI). *Journal of Child Psychology and Psychiatry and Allied Disciplines*, *42*, 741–748.
- Cowan, N. (2000). The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and Brain Sciences*, *24*, 87–185.
- Cowan, N., Li, D., Moffitt, A., Becker, T. M., Martin, E. A., Sauls, J. S., & Christ, S. E. (2011). A neural region of abstract working memory. *Journal of Cognitive Neuroscience*, *23*, 2852–2863.
- Dale, A. M., Fischl, B., & Sereno, M. I. (1999). Cortical surface-based analysis. I. Segmentation and surface reconstruction. *NeuroImage*, *9*, 179–194.
- Desikan, R. S., Segonne, F., Fischl, B., Quinn, B. T., Dickerson, B. C., Blacker, D., . . . Killiany, R. J. (2006). An automated labeling system for subdividing the human cerebral cortex on MRI scans into gyral based regions of interest. *NeuroImage*, *31*, 968–980.
- Dollaghan, C., & Campbell, T. F. (1998). Nonword repetition and child language impairment. *Journal of Speech, Language, and Hearing Research*, *41*, 1136–1146.
- Dufva, M., Niemi, P., & Voeten, M. J. M. (2001). The role of phonological memory, word recognition, and comprehension skills in reading development: From preschool to grade 2. *Reading and Writing*, *14*, 91–117.

- Ellis Weismer, S., Tomblin, J. B., Zhang, X., Buckwalter, P., Chynoweth, J. G., & Jones, M. (2000). Nonword repetition performance in school-age children with and without language impairment. *Journal of Speech, Language, and Hearing Research, 43*, 865–878.
- Fischl, B., van der Kouwe, A., Destrieux, C., Halgren, E., Segonne, F., Salat, D. H., . . . Dale, A. M. (2004). Automatically parcellating the human cerebral cortex. *Cerebral Cortex, 14*, 11–22.
- Frisch, S. A., Large, N. R., & Pisoni, D. B. (2000). Perception of word-likeness: Effects of segment probability and length on the processing of nonwords. *Journal of Memory and Language, 42*, 481–496.
- Gathercole, S. E. (1995). Is nonword repetition a test of phonological memory or long-term knowledge? It all depends on the nonwords. *Memory & Cognition, 23*, 83–94.
- Gathercole, S. E. (2006). Nonword repetition and word learning: The nature of the relationship. *Applied Psycholinguistics, 27*, 513–543.
- Gathercole, S. E., & Baddeley, A. D. (1990). Phonological memory deficits in language disordered children: Is there a causal connection? *Journal of Memory and Language, 29*, 336–360.
- Gathercole, S. E., & Baddeley, A. D. (1993). Phonological working memory: A critical building block for reading development and vocabulary acquisition? *European Journal of Psychology of Education, 8*, 259–272.
- Gathercole, S. E., & Baddeley, A. D. (1996). *The Children's Test of Nonword Repetition*. San Antonio, TX: The Psychological Corporation.
- Gathercole, S. E., Willis, C. S., Baddeley, A. D., & Emslie, H. (1994). The Children's Test of Nonword Repetition: A test of phonological working memory. *Memory, 2*, 103–127.
- Gorgolewski, K., Burns, C. D., Madison, C., Clark, D., Halchenko, Y. O., Waskom, M. L., & Ghosh, S. S. (2011). Nipype: A flexible, lightweight and extensible neuroimaging data processing framework in Python. *Frontiers in Neuroinformatics, 5*, 13. <https://doi.org/10.3389/fninf.2011.00013>
- Graf Estes, K., Evans, J. L., & Else-Quest, N. M. (2007). Differences in nonword repetition performance of children with and without specific language impairment: A meta-analysis. *Journal of Speech, Language, and Hearing Research, 50*, 177–195.
- Graves, W. W., Grabowski, T. J., Mehta, S., & Gupta, P. (2008). The left posterior superior temporal gyrus participates specifically in accessing lexical phonology. *Journal of Cognitive Neuroscience, 20*, 1698–1710.
- Greve, D. N., & Fischl, B. (2009). Accurate and robust brain image alignment using boundary-based registration. *NeuroImage, 48*, 63–72.
- Griffiths, T. D., & Warren, J. D. (2002). The planum temporale as a computational hub. *Trends in Neurosciences, 25*, 348–353.
- Hakim, H. B., & Ratner, N. B. (2004). Nonword repetition abilities of children who stutter: An exploratory study. *Journal of Fluency Disorders, 29*, 179–199.
- Hall, D. A., Haggard, M. P., Akeroyd, M. A., Palmer, A. R., Summerfield, A. Q., Elliot, M. R., . . . Bowtell, R. W. (1999). "Sparse" temporal sampling in auditory fMRI. *Human Brain Mapping, 7*, 213–223.
- Hartwigsen, G., Saur, D., Price, C. J., Baumgaertner, A., Ulmer, S., & Siebner, H. R. (2013). Increased facilitatory connectivity from the pre-SMA to the left dorsal premotor cortex during pseudoword repetition. *Journal of Cognitive Neuroscience, 25*, 580–594.
- Hasselhorn, M., & Körner, K. (1997). Nonword repetition: The role of working memory in the development of syntactical language abilities. *Zeitschrift für Entwicklungspsychologie und Pädagogische Psychologie, 29*, 212–224.
- Hein, G., & Knight, R. T. (2008). Superior temporal sulcus—It's my area: Or is it? *Journal of Cognitive Neuroscience, 20*, 2125–2136.
- Hickok, G. (2009). The functional neuroanatomy of language. *Physics of Life Reviews, 6*, 121–143.
- Hickok, G., Houde, J., & Rong, F. (2011). Sensorimotor integration in speech processing: Computational basis and neural organization. *Neuron, 69*, 407–422.
- Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience, 8*, 393–402.
- Hope, T. M. H., Prejawa, S., Parker Jones, O., Oberhuber, M., Seghier, M. L., Green, D. W., & Price, C. J. (2014). Dissecting the functional anatomy of auditory word repetition. *Frontiers in Human Neuroscience, 8*, 246.
- Jacquemot, C., & Scott, S. K. (2006). What is the relationship between phonological short-term memory and speech processing? *Trends in Cognitive Science, 10*, 480–486.
- Jäncke, L., Buchanan, T., Lutz, K., Specht, K., Mirzazade, S., & Shah, N. J. S. (1999). The time course of the BOLD response in the human auditory cortex to acoustic stimuli of different duration. *Cognitive Brain Research, 8*, 117–124.
- Jones, D. M., Hughes, R. W., & Macken, W. J. (2006). Perceptual organization masquerading as phonological storage: Further support for a perceptual-gestural view of short-term memory. *Journal of Memory and Language, 54*, 265–281.
- Jones, D. M., & Macken, W. J. (1993). Irrelevant tones produce an irrelevant speech effect: Implications for phonological coding in working memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 19*, 369–381.
- Jonides, J., Schumacher, E. H., Smith, E. E., Koeppe, R. A., Awh, E., Reuter-Lorenz, P. A., Marshuetz, C., & Willis, C. R. (1998). The role of parietal cortex in verbal working memory. *Journal of Neuroscience, 18*, 5026–5034.
- Jonides, J., Schumacher, E. H., Smith, E. E., Lauber, E. J., Awh, E., Minoshima, S., & Koeppe, R. A. (1997). Verbal working memory load affects regional brain activation as measured by PET. *Journal of Cognitive Neuroscience, 9*, 462–475.
- Kaufman, A. S., & Kaufman, N. L. (1990). *Kaufman Brief Intelligence Test*. Bloomington, MN: Pearson.
- Keren-Portnoy, T., Vihman, M. M., DePaolis, R. A., Whitaker, C. J., & Williams, N. M. (2010). The role of vocal practice in constructing phonological working memory. *Journal of Speech, Language, and Hearing Research, 53*, 1280–1293.
- Kjelgaard, M. M., & Tager-Flusberg, H. (2001). An investigation of language impairment in autism: Implications for genetic subgroups. *Language and Cognitive Processes, 16*, 287–308.
- Koenigs, M., Acheson, D. J., Barbey, A. K., Solomon, J., Postle, B. R., & Grafman, J. (2011). Areas of left perisylvian cortex mediate auditory-verbal short-term memory. *Neuropsychologia, 49*, 3612–3619.
- Lanfranchi, S., Jerman, O., & Vianello, R. (2009). Working memory and cognitive skills in individuals with Down syndrome. *Child Neuropsychology, 15*, 397–416.
- Larrivee, L. S., & Catts, H. W. (1999). Early reading achievement in children with expressive phonological disorders. *American Journal of Speech-Language Pathology, 8*, 118–128.
- Lawrence, M. A. (2012). ez: Easy analysis and visualization of factorial experiments. R package version 4.1-1. Available at <http://CRAN.R-project.org/package=ez>
- Laws, G., & Bishop, D. V. M. (2003). A comparison of language abilities in adolescents with Down syndrome and children with specific language impairment. *Journal of Speech, Language, and Hearing Research, 46*, 1324–1339.

- Leff, A. P., Schofield, T. M., Crinion, J. T., Seghier, M. L., Grogan, A., Green, D. W., & Price, C. J. (2009). The left superior temporal gyrus is a shared substrate for auditory short-term memory and speech comprehension: Evidence from 210 patients with stroke. *Brain*, *132*, 3401–3410.
- Linden, D. J. (2007). The working memory networks of the human brain. *The Neuroscientist*, *13*, 257–267.
- Loucas, T., Riches, N. G., Charman, T., Pickles, A., Simonoff, E., Chandler, S., & Baird, G. (2010). Speech perception and phonological short-term memory capacity in language impairment: Preliminary evidence from adolescents with specific language impairment (SLI) and autism spectrum disorders (ASD). *International Journal of Language & Communication Disorders*, *45*, 275–286.
- Lu, C., Qi, Z., Harris, A., Wisman Weil, L., Han, M., Halverson, K., ... Gabrieli, J. D. E. (2016). Shared neuroanatomical substrates of impaired phonological working memory across reading disability and autism. *Biological Psychiatry: Cognitive Neuroscience and Neuroimaging*, *1*, 169–177.
- MacNeilage, P. (2008). *The origin of speech*. Oxford, UK: Oxford University Press.
- Majerus, S. (2013). Language repetition and short-term memory: An integrative framework. *Frontiers in Human Neuroscience*, *7*, 357.
- Majerus, S., Collette, F., Van der Linden, M., Peigneux, P., Laureys, S., Delfiore, G., ... Salmon, E. (2002). A PET investigation of lexicality and phonotactic frequency in oral language processing. *Cognitive Neuropsychology*, *19*, 343–361.
- Markiewicz, C. J., & Bohland, J. W. (2016). Mapping the cortical representation of speech sounds in a syllable repetition task. *NeuroImage*, *141*, 174–190.
- Martin, R. C. (2005). Components of short-term memory and their relation to language processing: Evidence from neuropsychology and neuroimaging. *Current Directions in Psychological Science*, *14*, 204–208.
- McGettigan, C., Warren, J. E., Eisner, F., Marshall, C. R., Shanmugalingam, P., & Scott, S. K. (2011). Neural correlates of sublexical processing in phonological working memory. *Journal of Cognitive Neuroscience*, *23*, 961–977.
- Melby-Lervåg, M., Lervåg, A., Halaas Layster, S.-A., Klem, M., Hagtvet, B., & Hulme, C. (2012). Nonword-repetition ability does not appear to be a causal influence on children's vocabulary development. *Psychological Science*, *23*, 1092–1098.
- Metsala, J. L., & Chisholm, G. M. (2010). The influence of lexical status and neighborhood density on children's nonword repetition. *Applied Psycholinguistics*, *31*, 489–506.
- Montgomery, J. W. (1995). Examination of phonological working memory in specifically language-impaired children. *Applied Psycholinguistics*, *16*, 355–378.
- Munson, B. (2006). Nonword repetition and levels of abstraction in phonological knowledge. *Applied Psycholinguistics*, *27*, 577–581.
- Munson, B., Kurtz, B. A., & Windsor, J. (2005). The influence of vocabulary size, phonotactic probability, and wordlikeness on nonword repetitions of children with and without language impairments. *Journal of Speech, Language, and Hearing Research*, *48*, 1033–1047.
- Nithart, C., Demont, E., Majerus, S., Leybaert, J., Poncelet, M., & Metz-Lutz, M.-N. (2009). Reading disabilities in SLI and dyslexia result from distinct phonological impairments. *Developmental Neuropsychology*, *34*, 296–311.
- Page, M. P. A., Madge, A., Cumming, N., & Norris, D. G. (2007). Speech errors and the phonological similarity effect in short-term memory: Evidence suggesting a common locus. *Journal of Memory and Language*, *56*, 49–64.
- Papoutsis, M., de Zwart, J. A., Jansma, J., Pickering, M. J., Bednar, J. A., & Horowitz, B. (2009). From phonemes to articulatory codes: An fMRI study of the role of Broca's area in speech production. *Cerebral Cortex*, *19*, 2156–2165.
- Paulesu, E., Frith, C. D., & Frackowiak, R. S. J. (1993). The neural correlates of the verbal component of working memory. *Nature*, *362*, 342–345.
- Peelen, M. V., & Downing, P. E. (2006). Using multi-voxel pattern analysis of fMRI data to interpret overlapping functional activations. *Trends in Cognitive Sciences*, *11*, 4–5.
- Peeva, M. G., Guenther, F. H., Tourville, J. A., Nieto-Castanon, A., Anton, J.-L., Nazarian, B., & Alario, F.-X. (2010). Distinct representations of phonemes, syllables, and supra-syllabic sequences in the speech production network. *NeuroImage*, *50*, 626–638.
- Penfield, W., & Welch, K. (1951). The supplementary motor area of the cerebral cortex: A clinical and experimental study. *AMA Archives of Neurology and Psychiatry*, *66*, 289–317.
- Perrachione, T. K., & Ghosh, S. S. (2013). Optimized design and analysis of sparse-sampling fMRI experiments. *Frontiers in Neuroscience*, *7*, 55. <https://doi.org/10.3389/fnins.2013.00055>
- Peter, B., Raskind, W. H., Matsushita, M., Lisowski, M., Vu, T., Berninger, V. W., ... Brkanac, Z. (2011). Replication of *CNTNAP2* association with nonword repetition and support for *FOXP2* association with timed reading and motor activities in a dyslexia family sample. *Journal of Neurodevelopmental Disorders*, *3*, 39–49.
- Petrides, M., Alivisatos, B., Meyer, E., & Evans, A. C. (1993). Functional activation of human frontal cortex during performance of verbal working memory tasks. *Proceedings of the National Academy of Sciences, USA*, *90*, 878–882.
- Postle, B. R. (2006). Working memory as an emergent property of the mind and brain. *Neuroscience*, *139*, 23–38.
- Price, C., Thierry, G., & Griffiths, T. (2005). Speech-specific auditory processing: Where is it? *Trends in Cognitive Sciences*, *9*, 271–276.
- Raettig, T., & Kotz, S. A. (2008). Auditory processing of different types of pseudo-words: An event-related fMRI study. *NeuroImage*, *39*, 1420–1428.
- Rauschecker, A. M., Pringle, A., & Watkins, K. E. (2008). Changes in neural activity associated with learning to articulate novel auditory pseudowords by covert repetition. *Human Brain Mapping*, *29*, 1231–1242.
- Reuterskiöld-Wagner, C., Sahlén, B., & Nyman, A. (2005). Nonword repetition and non-word discrimination in Swedish preschool children. *Clinical Linguistics & Phonetics*, *19*, 681–699.
- Richardson, F. M., Ramsden, S., Ellis, C., Burnett, S., Megnin, O., Catmur, C., ... Price, C. J. (2011). Auditory short-term memory capacity correlates with gray matter density in the left posterior STS in cognitively normal and dyslexic adults. *Journal of Cognitive Neuroscience*, *23*, 3746–3756.
- Riches, N. G., Loucas, T., Baird, G., Charman, T., & Simonoff, E. (2011). Non-word repetition in adolescents with specific language impairment and autism plus language impairments: A qualitative analysis. *Journal of Communication Disorders*, *44*, 23–36.
- Rispens, J., & Baker, A. (2012). Nonword repetition: The relative contributions of phonological short-term memory and phonological representations in children with language and reading impairment. *Journal of Speech, Language, and Hearing Research*, *55*, 683–694.
- Rowe, J. B., Toni, I., Josephs, O., Frackowiak, R. S. J., & Passingham, R. E. (2000). The prefrontal cortex: Response selection or maintenance within working memory? *Science*, *288*, 1656–1660.

- Ruchkin, D. S., Grafman, J., Cameron, K., & Brendt, R. S.** (2003). Working memory retention systems: A state of activated long-term memory. *Behavioral and Brain Sciences*, *26*, 709–728.
- Schwepe, J., & Rummer, R.** (2007). Shared representations in language processing and verbal short-term memory: The case of grammatical gender. *Journal of Memory and Language*, *56*, 336–356.
- Smith, B.** (2006). Precautions regarding nonword repetition tasks. *Applied Psycholinguistics*, *27*, 584–587.
- Smith, E. E., Jonides, J., & Koeppe, R. A.** (1996). Dissociating verbal and spatial working memory using PET. *Cerebral Cortex*, *6*, 11–20.
- Smith, E. E., Jonides, J., Marshuetz, C., & Koeppe, R. A.** (1998). Components of verbal working memory: Evidence from neuroimaging. *Proceedings of the National Academy of Sciences, USA*, *95*, 876–882.
- Strand, F., Forssberg, H., Klingberg, T., & Norrelgen, F.** (2008). Phonological working memory with auditory presentation of pseudo-words—An event related fMRI study. *Brain Research*, *1212*, 48–54.
- Szenkovits, G., & Ramus, F.** (2005). Exploring dyslexics' phonological deficit I: Lexical vs sub-lexical and input vs output processes. *Dyslexia*, *11*, 253–268.
- Vaden, K. I., Jr., Piquado, T., & Hickok, G.** (2011). Sublexical properties of spoken words modulate activity in Broca's area but not superior temporal cortex: Implications for models of speech recognition. *Journal of Cognitive Neuroscience*, *23*, 2665–2674.
- Van Bon, W. H. J., & Van Der Pijl, J. M. L.** (1997). Effects of word length and wordlikeness on pseudoword repetition by poor and normal readers. *Applied Psycholinguistics*, *18*, 101–114.
- van der Schuit, M., Segers, E., van Balkom, H., & Verhoeven, L.** (2011). How cognitive factors affect language development in children with intellectual disabilities. *Research in Developmental Disabilities*, *32*, 1884–1894.
- Vitevich, M. S.** (2006). Manipulating the characteristics of words and nonwords to better understand word learning. *Applied Psycholinguistics*, *27*, 594–598.
- Vitevich, M. S., & Luce, P. A.** (2004). A web-based interface to calculate phonotactic probability for words and nonwords in English. *Behavior Research Methods, Instruments, and Computers*, *36*, 481–487.
- Wagner, R., Torgesen, J. K., & Rashotte, C.** (1999). *Comprehensive Test of Phonological Processing*. Austin, TX: Pro-Ed.
- Wildgruber, D., Ackermann, H., & Grodd, W.** (2001). Differential contributions of motor cortex, basal ganglia, and cerebellum to speech motor control: Effects of syllable repetition rate evaluated by fMRI. *NeuroImage*, *13*, 101–109.
- Wilson, L. B., Tregellas, J. R., Slason, E., Pasko, B. E., Hepburn, S., & Rojas, D. C.** (2013). Phonological processing in first-degree relatives of individuals with autism: An fMRI study. *Human Brain Mapping*, *31*, 1447–1463.
- Wilson, S. M., Isenberg, A. L., & Hickok, G.** (2009). Neural correlates of word production stages delineated by parametric modulation of psycholinguistic variables. *Human Brain Mapping*, *30*, 3596–3608.
- Woo, C. W., Krishnan, A., & Wager, T. D.** (2014). Cluster-extent based thresholding in fMRI analyses: Pitfalls and recommendations. *NeuroImage*, *91*, 412–419.
- Yoo, S., Chung, J.-Y., Jeon, H.-A., Lee, K.-M., Kim, Y.-B., & Cho, Z.-H.** (2012). Dual routes for verbal repetition: Articulation-based and acoustic-phonetic codes for pseudoword and word repetition, respectively. *Brain and Language*, *122*, 1–10.

Appendix A

Two-, four-, and six-syllable nonword and real-word stimuli. (Nonword pronunciation is shown in parentheses using International Phonetic Alphabet transcription.)

Nonwords

2-Syllable Nonwords

plever / pever ('plɛvə- / 'pɛvə-), penced / peced ('pɛnsɪd / 'pɛsɪd), tector / tetor ('tɛktə- / 'tɛtə-), mubler / muber ('mublə- / 'mubə-), sufting / sufing ('sʌftɪŋ / 'sʌfɪŋ), bicket / bippet ('bɪkɛt / 'bɪpɛt), blimpet / blimset ('blɪmpɛt / 'blɪmsɛt), nadle / naidle ('neɪdəl / 'naɪdəl), shoken / shopen ('ʃoukən / 'ʃoupən), sploiter / spleiter ('splɔɪtə- / 'splɛɪtə-), cranscow / cranksow ('krænskəu / 'krænskəu), troglem / trolgem ('trɔgləm / 'trɔlgəm), kolite / kilote ('kɔlɪt / 'kɔlɔt), preport / preprot ('pri:pɔrt / 'pri:prɔt), riftoon / roofin ('rɪftun / 'ruftɪn), priote ('praɪɔt), kabant ('kæbənt), ballom ('bæləm), kather ('kæðə-), gammert ('gæmə-t), shable ('ʃeɪbəl), morant ('mɔrənt), neaving ('nɪvɪŋ), klamic ('klæmɪk), ablit ('æblɪt), blekking ('blɛkɪŋ), dorson ('dɔrsən), quipid ('kwɪpɪd), yantel ('yæntəl), promin ('prɔmən)

4-Syllable Nonwords

icnidator / icidator ('ɪkni:deɪtə- / 'ɪki:deɪtə-), metretory / meretory ('mɛtrə:tɔri / 'mɛrə:tɔri), astragular / atragular (æ'strægjulə- / æ'trægjulə-), hibernatist / hiberatist (haɪ'bɜ:nə'tɪst / haɪ'bɜ:ə'tɪst), gasprodoxy / gasrodoxy ('gæsprəs,daksɪ / 'gæsrə,daksɪ), decepoment / decegoment (di'sɪpɔmənt / di'sɪgɔmənt), exvomit / exvotion (ɛksvou'mɪʃən / ɛksvou'tɪʃən), challopism / chollopism ('ʃælə,pɪzəm / 'ʃɔlɔ,pɪzəm), tralocistic / trallopistic (trælə'sɪstɪk / trælə'pɪstɪk), canastocize / canistocize (kæ'næstə,səz / kæn'ɪstə,səz), crimipism / cripimism ('krɪmɪ,pɪzəm / 'krɪpɪ,mɪzəm), matastrocy / mastatrocy (mə'tæstrə,sɪ / mə'stætrə,sɪ), candalopy / canladopy (kæn'dælə,pɪ / kæn'lædə,pɪ), besepalment / bepesimalment (bi'sɪpəlmənt / bi'pɪsəlmənt), reaquisment / reasquiment (ri'ækwɪzmənt / ri'æzkwɪmənt), hemostify (hi'moustəfaɪ), allotastry ('æləu,tæstri), shagonazle ('ʃæɡə,næzəl), kamastocize (kæ'mæstə,səz), rendoristat (rɛn'dɔrɪ,stæt), posidriate (pə'sɪdriət), benopify (bi'nɔpɪfaɪ), athandanate (æ'θændənɛɪt), nuplative (nu'plɛrətɪv), fandosity (fæn'dɔusɪtɪ), masadolyte (mæsædə,lɪt), kinimerate (kɪ'nɪmə-ɛɪt), cavanator ('kævə,nɛɪtə-), reostify (ri'oustrəfaɪ), illostratic (ɪlə'strætɪk)

6-Syllable Nonwords

hibiostydic / hibiosydic (hɪbiɔstə'dæɪtɪk / hɪbiɔsə'dæɪtɪk), creopleastify / creoleastify (kriɔpli'æstɪfaɪ / kriɔli'æstɪfaɪ), balerasticable / baleraticable (bælə'æstɪkəbəl / bælə'ætɪkəbəl), maderondastical / maderonastical (mædə-ɔn'dæstɪkəl / mædə-ɔ'næstɪkəl), tipcability / tipcibility (tɪpɪkə'bɪlɪtɪ / tɪpɪkə'bɪlɪtɪ), garomeandable / garomeansable (ɡeroumi'ændəbəl / ɡeroumi'ænsəbəl), realoosificate / realisificate (riə'lusəfɪkɛɪt / riə'ɪsəfɪkɛɪt), caterovyaling / cateromyaling (kætə-ɔ'vaɪəlɪŋ / kætə-ɔ'maɪəlɪŋ), effinitificate / effinitificate (ɛfɪnə'tɪfɪkɛɪt / ɛfɪnə'tuɪfɪkɛɪt), aggregotantable (æɡriə'tæntəbəl / æɡriə'pæntəbəl), ravinatoriness / ravinarotiness (rævɪnə'tɔrɪnəs / rævɪnə'rotɪnəs), atropianatry / atroniapatry (ætropi'ænɛɪtɪ / ætrɔni'æpɛɪtɪ), aleropenastic / aleronepastic (ælə-ɔpə'næstɪk / ælə-ɔnə'pæstɪk), delivreonating / deleneovrating (də'lɛvriəu,nɛɪtɪŋ / də'lɛniəu,vrɛɪtɪŋ), pasternaficity / pasterfanicity (pæstə-nə'fɪsɪtɪ / pæstə-fə'nɪsɪtɪ), cherotemianis (ʃɛrətə'maɪənəs), andoriatate (ændɔri'ætətɛɪt), malabanatoc (mə'læbənətɔsɪ), sonderaporeal (sɔndə-ə'pɔriəl), quibberachable (kwɪbə-ɛkɪəbəl), hyandomasity (haɪəndə'mæsɪtɪ), mikiokafitate (mɪkiə'kæfɪtɛɪt), pacheorianian (pɛɪkiə'reɪniən), imperiandicate (ɪmpɪri'ændəkɛɪt), piandification (pi'ændɪfə'keɪʃən), ecofabrility (ɪkofə'bɪlɪtɪ), heleomanity (hɪliə'mænɛɪtɪ), dorichiterizing (dɔ'rɪkɪtə-azɪŋ), acreodefentic (ækriədə'fɪntɪk), picaperilitate (pɪkəpə-ɪlɪtɛɪt)

Real Words

2-Syllable Real Words

annex, assent, ballot, blessing, deceit, decree, defense, despair, disgrace, distress, flourish, forfeit, franchise, frenzy, fullness, graphite, grievance, hobby, imprint, incline, insight, keeper, lecture, maker, marvel, mortal, mortar, omen, outpost, outset, pretense, retreat, revenge, romance, ruler, saga, seller, sorrow, thinker, token, treaty, turner, venture, veto, vigil

4-Syllable Real Words

adolescence, affirmation, apology, benefactor, bewilderment, catastrophe, certificate, complication, consolation, correspondence, dishonesty, dislocation, educator, enlightenment, expedition, geography, hesitation, immensity, immunity, imperfection, indication, infinity, intermission, interruption, invitation, irrigation, irritation, legality, neutrality, optimism, persecution, politician, prosperity, recollection, relaxation, respiratory, separation, solemnity, thermometer, uncertainty, undertaking, uneasiness, unhappiness, unpleasantness, zoologist

6-Syllable Real Words

acceptability, accountability, advisability, availability, characterization, compressibility, denominational, differentiation, discontinuity, diversification, ecclesiastical, eligibility, excitability, externalization, familiarity, generalization, homogeneity, identifiable, identification, illegitimacy, impartiality, inferiority, insubordination, intensification, interplanetary, irrationality, irreconcilable, irregularity, meteorological, originality, personification, psychoanalysis, reconsideration, rehabilitation, reliability, reorganization, republicanism, respectability, responsibility, revolutionary, superiority, uninitiated, universality, unsatisfactory, vulnerability

Appendix B

Details of Phonological Manipulations in Nonmatching Nonword Pairs

No. Syllables	Type of error	Affected syllable						Syllable position				Changed features			
		1	2	3	4	5	6	Onset	Cluster	Nucleus	Coda	Place	Manner	Place + manner	Vowel quality
2	Deletion	3	2	—	—	—	—	2	1	0	2	—	—	—	—
	Replacement	2	3	—	—	—	—	3	0	2	0	2	0	1	2
	Transposition	4	5	—	—	—	—	0	2	3	0	—	—	—	—
	Total	9	10	—	—	—	—	5	3	5	2	2	0	1	2
4	Deletion	0	4	1	0	—	—	2	3	0	0	—	—	—	—
	Replacement	1	1	3	0	—	—	3	0	2	0	1	0	2	2
	Transposition	0	5	5	0	—	—	5	0	0	0	—	—	—	—
	Total	1	10	9	0	—	—	10	3	2	0	1	0	2	2
6	Deletion	0	1	1	3	0	0	1	4	0	0	—	—	—	—
	Replacement	0	0	1	3	1	0	3	0	2	0	1	1	1	2
	Transposition	0	0	3	4	3	0	5	0	0	0	—	—	—	—
	Total	0	1	5	10	4	0	9	4	2	0	1	1	1	2
Total		10	21	14	10	4	0	24	10	9	2	4	1	4	6

Note. Em dash indicates syllable or feature could not be affected by a particular error type.