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Lexical mediation of phonotactic frequency effects on spoken word recognition: A Granger causality analysis of MRI-constrained MEG/EEG data

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Abstract

Phonotactic frequency effects play a crucial role in a number of debates over language processing and representation. It is unclear however, whether these effects reflect prelexical sensitivity to phonotactic frequency, or lexical “gang effects” in speech perception. In this paper, we use Granger causality analysis of MR-constrained MEG/EEG data to understand how phonotactic frequency influences neural processing dynamics during auditory lexical decision. Effective connectivity analysis showed weaker feedforward influence from brain regions involved in acoustic-phonetic processing (superior temporal gyrus) to lexical areas (supramarginal gyrus) for high phonotactic frequency words, but stronger top-down lexical influence for the same items. Low entropy nonwords (nonwords judged to closely resemble real words) showed a similar pattern of interactions between brain regions involved in lexical and acoustic-phonetic processing. These results contradict the predictions of a feedforward model of phonotactic frequency facilitation, but support the predictions of a lexically mediated account.

Keywords

phonotactic frequency; lexical neighborhood; effective connectivity; magnetoencephalography; Granger causation; speech perception; lexical effect

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Introduction

This paper explores the dynamic relationship between the perception of words and speech sounds. Evidence from a variety of behavioral, BOLD imaging and electrophysiological paradigms demonstrates that spoken word recognition is influenced by phonotactic frequency, a measure of how many words share a specific phoneme or sequence of phonemes in a particular position (cf. Luce & Pisoni, 1998; Pitt & Samuel, 1995; Vitevitch & Luce, 1998a; Vitevitch & Luce, 1999). Our sensitivity to phonotactic frequency is considered key evidence for understanding both the functional architecture of spoken word recognition processes (Magnuson, McMurray, Tanenhaus, & Aslin, 2003a; McQueen, 2003; McQueen, Jesse, & Norris, 2009; Pitt & McQueen, 1998; Samuel & Pitt, 2003), and the fundamental representational constraints that shape phonology (Albright, 2009; Hay, Pierrehumbert, & Beckman, 2004; Hayes & Wilson, 2008). In this paper, we examine how phonotactic frequency manipulations influence dynamic interactions between brain regions involved in lexical and acoustic-phonetic representation during spoken word recognition.

Phonotactic Frequency Effects

The distribution and frequency of linguistic structures affects language processing in many ways. Early psycholinguistic studies found that listeners are sensitive to lexical frequency in spoken word recognition (Pollack, Rubenstein, & Decker, 1959; Savin, 1963). Subsequent work has shown that humans are sensitive to the relative frequency of linguistic units in almost every aspect of language acquisition, perception and production (see review by Ellis, 2002). A second wave of interest in frequency, or more specifically transitional probability, the relative frequency with which one element follows another, occurred following Saffran et al.'s seminal work showing that even brief exposure to manipulations of transitional probability influences the way very young children segment the speech stream (Saffran, 2003; Saffran, Aslin, & Newport, 1996).

Words composed of more frequent phonological constituents generally enjoy a processing advantage (Pitt & Samuel, 1995; Vitevitch & Luce, 1999). Understanding why phonotactic frequency influences processing is important because these biases play a crucial role in competing accounts of language processing and representation. Crucially, they suggest an alternate account of results that have been interpreted as evidence for online top-down lexical influences on speech perception. Elman and McClelland demonstrated that ambiguous word-final fricatives whose interpretation appears to be influenced by lexical context can drive low-level perceptual compensation for coarticulation (Elman & McClelland, 1988). Since the publication of that work, a number of studies have tried to determine whether this phenomenon is due to online top-down lexical influences that perceptually “restore” missing phonemes, or bottom-up perceptual or mapping processes that favor phonotactic patterns that occur in many words (Cairns, Shillcock, Chater, & Levy, 1995; Magnuson et al., 2003a; Magnuson, McMurray, Tanenhaus, & Aslin, 2003b; McQueen, 2003; McQueen et al., 2009; Pitt & McQueen, 1998; Samuel & Pitt, 2003). Phonotactic frequency is a reflection of the structure of the lexicon. The bottom-up account suggests that “lexical influences” on speech perception develop offline as biases that favor the perception or feedforward mapping of more common phonotactic patterns from acoustic-

phonetic to lexical representations. This work has shown that the crucial behavioral phenomena are fragile and may be influenced by a variety of methodological factors. There is still no consensus about which view is correct.

It is hard to study phonotactic frequency effects independently because they are often masked by the inhibitory effects of phonological neighborhood size (Pisoni, Nusbaum, Luce, & Slowiaczek, 1985), a variable highly correlated with phonotactic frequency (Frauenfelder, Baayen, & Hellwig, 1993). Words composed of more common sublexical constituents that also have large neighborhoods (hereafter referred to as high phonotactic frequency-density) produced slower responses in tasks including shadowing, lexical decision, and speeded same-different judgment, than words with small neighborhoods composed of less frequent elements (Dufour & Frauenfelder, 2010; Vitevitch & Luce, 1998b; Vitevitch & Luce, 1999; Vitevitch, Luce, Pisoni, & Auer, 1999). Both phonotactic frequency and lexical neighborhood are defined by phonological patterning in the lexicon, and may be considered measures of lexical similarity with phonotactic frequency reflecting partial overlap, and neighborhood size reflecting more complete overlap with words represented in the lexicon. When phonotactic frequency and neighborhood density are varied orthogonally, phonotactic frequency effects are clearer. Words with more common phonotactic components produce better performance in speeded same-different judgments than words with less common components (Luce & Large, 2001). Phonotactic frequency effects are more complex when nonword stimuli are used. High (phonotactic) frequency-density nonwords produce slower lexical decision, but present faster shadowing and speeded same-different judgments, which reverses many of the word findings (Vitevitch & Luce, 1998b; Vitevitch & Luce, 1999; Vitevitch & Luce, 2005). Other studies have shown that these results are at least partially attributable to a systematic correlation between neighborhood size and word duration (Lipinski & Gupta, 2005). The one study that deconfounded neighborhood size and phonotactic frequency found no significant effects for either variable in nonword same-different judgment reaction times. A follow up experiment found faster responses for higher phonotactic frequency nonwords, but only when targets were judged to resemble relatively few real words (Luce & Large, 2001).

The dissociation between phonotactic frequency and phonological neighborhood effects has been interpreted in a framework that attributes neighborhood effects to lexical competition and phonotactic frequency effects to sublexical (e.g. phoneme or biphone) phenomena (cf. Luce & Pisoni, 1998; Pytkänen, Stringfellow, & Marantz, 2002; Vitevitch & Luce, 1998a; Vitevitch & Luce, 1999; Vitevitch et al., 1999). The literature on lexical frequency effects suggests a number of computationally plausible mechanisms that might be adapted to explain phonotactic frequency effects. These include frequency-sensitive recognition thresholds (Morton, 1969), frequency indexed resting activation levels (Marslen-Wilson, 1990), or frequency-determined priors operating within a Bayesian classifier (Norris & McQueen, 2008).

Another possibility is that phonotactic frequency effects are the result of mapping between acoustic-phonetic representation and lexical representation. Phonotactic frequency could be encoded in the connection weights linking feedforward mapping to lexical representation. This strategy is implemented in some connectionist modeling (Seidenberg & McClelland,

1989), and is consistent with physiological evidence favoring Hebbian learning (Carew, Hawkins, Abrams, & Kandel, 1984; Hebb, 1949). Alternatively, top-down lexical “gang” influences on lower acoustic-phonetic or phonological processing could produce facilitatory effects on word recognition by strengthening lower level speech representations that overlap with more lexical candidates. The benefit to high phonotactic frequency words from the stronger cumulative positive feedback produced by larger cohorts of words with common patterns could coexist with lexical competition. This interpretation is consistent with perceptual studies showing that the categorization of phonemes in nonword contexts is influenced by the degree to which phonotactic patterns overlap with lexical candidates (Newman, Sawusch, & Luce, 1997). Further support coming from effective connectivity analyses shows that biases in phoneme categorization favoring phonotactically legal interpretations are associated with increased influence of the supramarginal gyrus, a region associated with lexical representation, on activation in superior temporal regions associated with acoustic-phonetic representation (Gow & Nied, 2014). While this result was found using nonword stimuli, it closely matches effective connectivity patterns associated with behavioral evidence for lexical influences on speech categorization (Gow, Segawa, Ahlfors, & Lin, 2008).

Interactive processing remains a controversial topic in speech recognition. A large body of behavioral results demonstrate that lexical and acoustic-phonetic factors both influence phonological judgments (cf. Connine & Clifton, 1987; Ganong, 1980; Marslen-Wilson & Warren, 1994; Newman et al., 1997; Warren, 1970). However, because this work only examines the output of processing, it is unclear whether this combined influence reflects interactive processing (direct lexical influences on perceptual processing), or the mutual effects of lexical and acoustic-phonetic analyses on post-perceptual response selection (Norris, McQueen, & Cutler, 2000). Several studies have addressed this limitation by examining the influence of lexically “restored” phonemes on low-level perceptual adaptation and context effects (Elman & McClelland, 1988; Magnuson et al., 2003a; Magnuson et al., 2003b; Samuel, 1997, 2001; Samuel & Pitt, 2003). In these studies, phonemes are typically excised from recordings of words, and replaced by noise. Listeners report hearing the missing sounds. Moreover, these restored sounds produce behavioral effects believed to have a phonetic locus. These results appear to support interactive processing. This interpretation has been challenged in a series of results and methodological critiques arguing that adaptation effects have a post-perceptual locus, and that critical context effects may be attributable to either perceptual learning and/or feedforward mapping processes that are sensitive to diphone frequency (McQueen, 2003; McQueen et al., 2009; Norris et al., 2000). This work has been met by a series of empirical studies that challenge these claims (Magnuson et al., 2003a; Magnuson et al., 2003b; Samuel, 2001; Samuel & Pitt, 2003). The field remains deeply divided despite the intensity and creativity of behavioral work completed on both sides of the interactivity debate.

The question of whether phonotactic frequency effects are lexical or prelexical has been addressed behaviorally most directly through studies that examine the timecourse of processing. A sequential processing model suggests that prelexical effects should occur before lexical effects. Several studies have addressed this question by contrasting the timecourse of recognition for words and nonwords with high versus low phonotactic

frequency-density. Pylkkänen et al. (2002) attempted to pull these variables apart by contrasting the facilitatory effects of phonotactic frequency with the inhibitory effects of neighborhood size. They reasoned that the facilitation associated with increased phonotactic frequency should reduce the latency of the M350 MEG component, while the inhibition associated with increased neighborhood density should increase M350 latency. They found reduced M350 latency for high phonotactic frequency/large neighborhood words and nonwords, and concluded that the M350 indexed prelexical phonotactic frequency effects, but not post-lexical neighborhood effects.

This interpretation is problematic on three grounds. First, analyses of peak latency, especially those based on grand averaged waveforms, are controversial because refraction between multiple generators and averaging artifacts are known to influence waveform topology (Coles & Rugg, 1995; Luck, 2005). Second, the predictions are only meaningful if neighborhood and phonotactic frequency effects are temporally separable. If they overlap in time, the latency of the M350 may index their cumulative effects. In this case, it might mean that phonotactic facilitation effects are stronger than overlapping neighborhood effects during this epoch. Finally, the latency of M350, measured in the interval between 300–400 ms post onset, places it after the likely onset of lexical activation, which is estimated to be close to 200 ms based on evidence from auditory gating, fragment priming, and eyetracking (Allopenna, Magnuson, & Tanenhaus, 1998; Magnuson, Dixon, Tanenhaus, & Aslin, 2007a; Marslen-Wilson, 1990; Marslen-Wilson & Zwitserlood, 1989). Other ERP studies have shown earlier sensitivity to phonotactic frequency-density manipulations including the phonological mismatch negativity (PMN) (250–330 ms) (Dufour, Brunelliere, & Frauenfelder, 2013), and P2/P200 (190–250 ms) (Cheng, Schafer, & Riddell, 2014; Hunter, 2013). All of these results suggest that phonotactic frequency or phonological neighborhood sensitivity has a timecourse that closely parallels lexical access. The notion that these effects are related to lexical activation is further supported by Prabhakaran et al.'s finding (2006) that words with high phonotactic frequency and dense phonological neighborhoods produce increased activation of the SMG, a region implicated in lexical processing by a convergence of evidence from BOLD imaging, aphasiology and neuroanatomy (Gow, 2012).

Dufour et al. (2013) provide the strongest evidence that phonological neighborhood and density effects have different timecourses. They found that simultaneous manipulation of phonotactic frequency-density influenced the amplitude of both the PMN and the late N400 (550–650 ms). They suggest that the earlier component reflects phonotactic frequency and the latter component reflects neighborhood driven competition effects. This interpretation of the earlier component is consistent with results showing that initial phoneme frequency, a phonotactic frequency measure, influences the latency of the P2 component (Hunter, 2013), and Pylkkänen et al.'s (2002) interpretation of their results. Hunter did not examine the effects of phonotactic frequency-neighborhood during the late N400 interval, but did find sustained effects of these manipulations during a 370–430 ms window. Because none of these experiments manipulated neighborhood density and phonotactic probability independently, it is not clear how later potentials should be interpreted. Nevertheless, from a computational perspective, one might expect neighborhood effects to have a longer rise time, simply because the neighborhood is not fully defined until listeners have heard an

entire word. In contrast, lexically-mediated phonotactic frequency effects could begin to emerge as soon as there is any overlap between speech input and a cohort or gang of phonologically overlapping lexical candidates.

Collectively, these results do not clearly establish whether phonotactic frequency effects result from lexical or prelexical mechanisms. This is a common problem that results from the inherent inability of behavioral, BOLD imaging and evoked component data to reliably discriminate between modular and interactive functional architectures (Dennett, 1992; Gow & Caplan, 2012; Norris et al., 2000).

Research Plan

The goal of the current study is to examine the functional relationship between lexical and acoustic processing by observing the effects of phonotactic frequency manipulations. Our strategy is to compare patterns of effective connectivity (directed causation between brain regions) while subjects performed an auditory lexical decision task involving words and nonwords with high versus low cumulative phonotactic frequency, restricting our focus to items with low neighborhood density. We restricted our analysis to items matched for low neighborhood density for several reasons. Previous behavioral results demonstrate that neighborhood and phonotactic effects are separable, and show that phonotactic frequency effects are largest for words and low entropy nonwords with small phonological neighborhoods (Luce & Large, 2001). Luce and Large note that neighborhood effects tend to be inhibitory, and so may mask excitatory phonotactic frequency effects. Moreover, large neighborhood items pose particular challenges for effective connectivity analyses. Inhibitory neighborhood effects are widely attributed to competition between strongly activated lexical candidates (cf. Luce & Pisoni, 1998; Magnuson, Dixon, Tanenhaus, & Aslin, 2007b; Norris, 1994; Vitevitch & Luce, 1998a). If competing lexical candidates are represented within a brain region, our analysis (which only examine dynamic interactions between discrete areas) will not be sensitive to their competitive influences.

We measured effective connectivity using a variant of Granger causality analysis (Geweke, 1982; Granger, 1969) that relies on Kalman filter techniques (Gow & Caplan, 2012; Milde et al., 2010). Granger causality analysis identifies statistical patterns that are consistent with directed causal interaction between variables. It is built on the intuition that causes both precede and uniquely predict their effects. It is computed by creating predictive models, in this case using a Kalman filter, that draw on timeseries data from of all potentially causal variables to predict the future behavior of a single variable. Unique causality is assessed by comparing the error terms associated with models based on all variables, with those of models in which one (putatively causal) variable has been removed. If the error term is significantly larger when a predictor variable is removed, that variable is said to Granger cause changes in the predicted variable. Computationally, Granger causation is a form of information transfer (transfer entropy for Gaussian variables) between stochastic processes (Barnett, 2009). In a neural context, this information may be thought of as *resolving* a specific pattern of localized activation corresponding to a representation.¹

The logic of Granger causation places important constraints on the identification of brain regions to include in these analyses. The requirement to include all non-redundant, potentially causal variables mitigates for the use of data driven techniques to identify brain regions of interest (ROIs). Theory driven ROI selection is problematic because current neuroanatomical models are generally incomplete, and fail to account for activation differences reflecting individual differences in functional localization, strategy, and task effects. For that reason, ROI selection is entirely data-driven to ensure the integrity of our Granger analyses (Gow & Caplan, 2012). Because different conditions typically produce different activation patterns, we identified a different set of ROIs for different conditions using the same automated process. It should be noted that ROIs are identified based on activity over time. As a result, even ROIs that reflect low level perceptual processing may show different patterns of localization due to interactions with other ROIs associated with later emerging processes or representations that may boost or depress their mean activation over time.

We applied these analyses to source space reconstructions of MRI-constrained simultaneous MEG/EEG data collected during task performance. We chose this imaging approach because it provides sufficient spatial resolution to associate activation with functionally interpretable brain regions (Sharon, Hämäläinen, Tootell, Halgren, & Belliveau, 2007), covers all cortical regions simultaneously, and provides the temporal resolution and sampling rate (<1 ms) required to support meaningful event-related timeseries analysis (Gow & Caplan, 2012).

Working from a neuroanatomical framework that attributes activation in bilateral STG to acoustic-phonetic processing (Hickok & Poeppel, 2004, 2007; Price, 2010) and the supramarginal gyrus (SMG) and posterior middle temporal gyrus (pMTG) to lexical representation (Gow, 2012; Hickok & Poeppel, 2007), we made the following predictions. If phonotactic frequency facilitation has a prelexical locus, high phonotactic frequency items should facilitate acoustic-phonetic processing, which in turn should facilitate feedforward mapping to lexical representations. This should produce stronger influences of acoustic-phonetic areas on activation of lexical regions than lower phonotactic frequency items should. If phonotactic frequency facilitation is a gang effect produced by top-down influences on acoustic-phonetic processing by a set of lexical candidates with overlapping phonotactic patterns, high phonotactic frequency items should produce stronger influences by lexical regions on acoustic-phonetic regions than lower phonotactic frequency items do. We made these predictions recognizing that lexical decision is a complex metalinguistic task, and processing may involve both, none or either of these mechanisms in concert with task specific processes.

¹There is a somewhat complicated relationship between Granger causation and measures of raw brain activation. While Granger causation reflects decreased uncertainty about the future activation pattern of a brain region (which may be globally strong or weak), ambiguity itself is often associated with increased activation of brain regions. Strong Granger effects therefore do not necessarily predict or reflect strong cortical activation.

Materials and Methods

Participants

Fourteen right-handed native speakers of American English with no discernible auditory processing deficits participated in the study. They ranged in age from 19–53 (mean age 24.7 years) and included five females. All participants provided informed consent following an IRB protocol approved by the Massachusetts General Hospital. Of the fourteen original subjects, one was dropped from the analysis due to illness-related poor behavioral performance (accuracy < 85%), and another was dropped due to equipment malfunction.

Materials

The experimental stimuli consisted of 180 consonant-vowel-consonant (CVC) tokens developed by Luce and Large (2001). They included an equal number of words and nonwords with small phonological neighborhoods that varied in cumulative phonotactic frequency. There were also 180 distractor CVC tokens including equal numbers of high and low phonotactic frequency words and nonwords with large phonological neighborhoods taken from the same study. Lexical statistics were derived from a 20,000 word online lexicon based on Webster's Pocket Dictionary (Luce & Pisoni, 1998) with lexical frequency statistics derived from Kuera and Francis (1967). Phonotactic frequency was defined for each item by the product of each phoneme's positional frequency (words: mean high frequency = 1.35×10^{-4} , mean low frequency = 0.03×10^{-4} ; nonwords: mean high frequency = 1.5×10^{-4} , mean low frequency = 0.45×10^{-4}) as well as the product of position-specific biphone frequency for the 2 biphones that form each CVC (words: mean high frequency = 1.55×10^{-5} , mean low frequency = 0.4×10^{-5} ; nonwords: mean high frequency = 1.7×10^{-5} , mean low frequency = 0.5×10^{-5}). Neighborhood size was operationalized as the cumulative log frequency of all words in the lexicon that could be formed by a single phoneme substitution, deletion or addition in any position (words: mean large neighborhood = 2.4, mean small neighborhood = 2.25; nonwords: mean large neighborhood = 2.35, mean small neighborhood = 2.2). The use of positional frequency to help define phonotactic frequency meant that high and low phonotactic frequency items also differed significantly in average initial cohort size, and incidentally in average cohort (log) frequency. Additional statistics are reported in Luce and Large (2001). Our design crossed phonotactic frequency (high versus low) with lexicality (word versus nonword) yielding four conditions, with 45 items per condition (see Appendix).

In previous work using these stimuli (Luce & Large, 2001), phonotactic frequency effects on reaction time were only found in words, and a subset of nonwords judged to have low entropy. Entropy is a subjective measure of the number of lexical competitors a nonword has. We identified a comparable set of low entropy nonwords for additional analyses using methods adapted from Luce and Large (2001). Nineteen native English speakers with no reported hearing deficits listened to the low-neighborhood density nonwords used in the study, and were asked to generate a similar word after hearing each. We rank ordered the number of different words subjects generated in response to each item and performed a median split within the high and low phonotactic frequency items to identify low and high

entropy items within each set. Items that generate fewer different word responses were identified as low entropy nonwords. Low entropy nonwords are marked in the appendix.

All tokens were recorded in citation form by a phonetically trained male reader in a quiet environment and were digitized at a sampling rate of 44.1 kHz as 16 bit sound. These stimuli were subsequently normalized for intensity and duration (500 ms) using Praat (Boersma & Weenink, 2011).

Procedure

We collected behavioral data in a single testing session, conducted in a three-layer magnetically shielded room (Imedco, Hägendorf, Switzerland). We simultaneously acquired magnetoencephalographic (MEG) and electroencephalographic (EEG) data while the subjects performed the behavioral task. Anatomical MRI data were collected immediately after this session. Each of the 360 trials began with the 500 ms presentation of a visual fixation stimulus (“+”) on a projection screen, followed by the auditory presentation of a single word/nonword delivered via MEG-compatible pneumatic tube earphones at a comfortable listening volume. The fixation remained on-screen throughout auditory stimulus presentation to minimize electrophysiological artifacts due to excessive eye movements. Subjects were instructed to decide whether each token was a word or nonword, and to indicate their judgment by button-press with their non-dominant hand using two response keys. They were also asked to blink only immediately after making a button-press so that eye movement artifacts would not influence MEG data collected during task performance. In a departure from behavioral testing norms, responses were self-paced and subjects were not instructed to respond as quickly as possible. This precluded reaction time analyses, but was intended to maximize the temporal separation between the early automatic speech recognition processes that are the focus of this work, and task-specific response selection processes that we hypothesize would dominate processing as subjects make their behavioral responses.

MEG and MRI Acquisition

The MEG and EEG data were collected using a whole head Neuromag Vectorview system (Elekta, Helsinki, Finland). This system has 306 MEG channels, and receives input from a 70 channel EEG cap with a nose reference, shoulder ground, and electro-oculogram (EOG) inputs to identify potential electrophysiological artifacts from vertical and horizontal eye movements and blinks. The MEG channels include 204 planar gradiometers and 102 magnetometers. We recorded MEG and EEG data at a sampling rate of 1209.83 Hz after filtering between 0.1 and 400 Hz. Representative EOG artifacts were identified by visual inspection of individual subject EOG and MEG channel data. Using a principle components analysis (PCA) technique, we created filters for each subject and projected out potential EOG artifacts. Prior to testing we identified the position of all scalp electrodes and four head position indicator coils, as well as 100 surface points on the scalp relative to three anatomical reference points (the nasion and two auricular landmarks) using a FastTrack 3D digitizer (Polhemus, Colchester, VT). During testing, head position within the MEG sensor array was tracked using the position of the head-position indicator coils.

We collected anatomical MRI data to provide realistic anatomical constraints for MEG/EEG source construction, and to facilitate the visualization of source reconstructions over cortical surfaces. MRI data were acquired using a 1.5 T Avanto 32 channel “TIM” system. We constructed high-resolution 3D T1-weighted anatomical images using an MPRAGE sequence (TR = 2730 ms, T1 = 1000 ms, TE = 3.31 ms, flip angle = 7°, FOV = 256 mm, slice thickness = 1.33 mm).

Source Reconstruction

We combined MEG, EEG and MRI data to create high spatiotemporal resolution anatomically constrained MEG activation movies. This approach provides source localization that is better than that of unimodal MEG or EEG analyses or of standard fused fMRI/MEG techniques (Sharon et al., 2007). For each subject, the cortical surface was reconstructed as approximately 300,000 vertices over a tessellated surface using Freesurfer (Dale, Fischl, & Sereno, 1999; Fischl, Sereno, & Dale, 1999; Segonne et al., 2004). This representation was decimated by a factor of 25 to yield approximately 12,000 vertices that served as potential dipole locations in subsequent MEG/EEG source analyses (Dale & Sereno, 1993). The outer and inner surfaces of the skull were also identified in Freesurfer. These were applied to the Boundary Element Model (BEM) that was used in the MEG/EEG forward model for source localization (Hämäläinen & Sarvas, 1989). The MRI reconstruction was aligned with the MEG/EEG coordinate system using the fiducial landmarks and head surface points identified prior to MEG testing.

We used minimum norm estimates (MNE) to reconstruct brain activity based on MEG/EEG data (Hämäläinen & Ilmoniemi, 1984) using the MNE software package (<https://www.martinos.org/mne/>) and Matlab programs based on MNE. MNE activation movies were created for all experimental conditions. MRI-constrained MEG/EEG reconstructions were made based on individual subject data, and then were averaged using a spherical morphing technique (Fischl, Sereno, Tootell, & Dale, 1999). These produced maps of low-pass filtered (at 60 Hz) average activity over an averaged cortical surface. We used inflated cortical surfaces to enhance the visualization of activity within the sulci (Fischl, Sereno, & Dale, 1999).

Region of Interest Identification

ROIs were defined using an algorithm based on the similarity and strength of MNE activation time series at each vertex over the cortical surface over the period between 100 and 500 ms after the onset of stimulus presentation. Separate sets of ROIs were identified using the same criteria for all word and nonword trials using group-averaged reconstructions of cortical activity.

ROIs were identified in three steps. First, vertices showing mean activation (averaged over all subjects and the 100–500 ms time window) over the 95th percentile were identified as potential centroids for ROIs. Vertices within 7 mm of local maxima were excluded to reflect a conservative estimate of the spatial resolution of source reconstructions (Sharon et al., 2007). Next, we quantified the similarity between activation at pairs of vertices by calculating the difference between the Euclidean norms of their activation functions. ROIs

with homogenous activation functions were grown from these centroids by comparing activation at contiguous vertices using this metric. Vertices with difference measures within 0.5 standard deviations of the centroid's activation function were included. We identified these regions to account for small intersubject differences in localization that could influence the selection of optimal representative vertices in each ROI for each subject in subsequent analyses. Finally, because Granger analysis is concerned with the unique information carried by each signal, it was necessary to eliminate any redundant ROIs. We did this by pairwise comparison of all ROIs using the same similarity metric. When two ROIs differed by less than 0.9 standard deviations (based on the activation function of the stronger ROI) the weaker ROI was excluded.

Kalman Filter-Based Granger Analysis

Effective connectivity was measured using an implementation of Granger causality (Geweke, 1982; Granger, 1969) that relies on Kalman filter techniques for predictive modeling (Milde et al., 2010). Kalman filter techniques have several advantages in this context. Kalman filters provide time-varying models, obviating the need for unrealistic assumptions about the stationarity of evoked neural signals, and making it possible to track Granger causality at each time point. Moreover, Kalman filters offer robust estimation given noisy measurement techniques. We created averaged timeseries for each subject and condition for every ROI. These were based on the vertex within each ROI that showed the highest mean activation for each subject. Within a condition and from every individual participant, the averaged MNE measures of activity from all of the ROIs were passed through a multi-trial Kalman filter to predict activity in a single target ROI (X). Next, a counter model to predict X was created excluding one ROI (Y) from the set of predictor variables. All models made predictions at each time point with a lag of 5 samples. This lag was determined heuristically after both Akaike and Bayesian Information Criteria failed to identify a single optimal model order. This modeling approach was used iteratively at each timepoint and for all combinations of predicted (X) and excluded (Y) ROIs. In all cases models showed strong convergence with 80 ms. As such, analyses focused on effective connectivity beginning 100 ms after the onset Kalman modeling.

The strength of Granger causality was quantified as the log ratio of standard prediction errors for the full model (using all ROIs to predict the future behavior of ROI X), and the restricted model created by taking out one predictor (Y). If the model that excludes Y has a greater standard prediction error than the model that includes Y, it can be inferred that the presence of Y in the model carries some unique predictive information, and thus region Y is said to Granger cause changes in X. This measure, Granger Causality Index (GCI) was computed at each timepoint for every potential directed interaction between ROIs. A bootstrapping method was used to determine the p value of each GCI measure (Milde et al., 2010). This involved comparing observed GCI values to a null distribution of GCI values for each observation based on 2000 trials of data reconstructed from Kalman matrices excluding the potentially causal ROI and randomizing the residuals. Comparisons were made between conditions over a common set of ROIs using a binomial test (Cho & Campbell, 2000) that compared the number of timepoints in each condition that produced GCI observations with

p-values less than 0.05. These comparisons are our primary results. The timecourses of key directed interactions between ROIs in each condition are reported as supplementary data.

Results and Discussion

Behavioral Results

The behavioral results are shown in Fig. 1. Analyses of accuracy showed a significant main effect for lexicality, $F(1,11) = 5.78$, $p < 0.05$, $d = 0.5$. Lexicality did not interact with other variables. We found no significant main effects or interactions involving phonotactic frequency or neighborhood size in accuracy analyses. Contrast analyses revealed no significant effects of phonotactic frequency for either the WORD or NONWORD conditions. A second set of analyses used measures derived from signal detection theory (d' and c) to address potential between-condition differences in sensitivity and response bias (MacMillan & Creelman, 2005). These were not able to address lexicality effects, which depend on responses to both word and nonword trials. They revealed no significant effects of phonotactic frequency on sensitivity or response bias in the task. Analyses focusing exclusively on low entropy nonwords similarly showed a slight accuracy advantage for high phonotactic frequency items compared to low phonotactic frequency items (89.8% versus 86.5% correct), but this did not reach statistical significance ($t(11) = 1.39$, $p > 0.05$). Our failure to find effects of phonotactic frequency on accuracy data is consistent with the accuracy analyses of Luce and Large (2001). Reaction time analyses were not attempted because the task employed non-speeded responses to maximize the dissociation between neural processes related to spoken word perception and lexical decision performance. The average response latency of 1185 ms placed responses more than 500 ms after the end of the 100–500 ms window that was the focus of neural analyses. This does not preclude a role of task-specific response selection processes during the 100–500 ms interval of interest. However, in the absence of any incentive to delay behavioral responses, these results suggest that response selection evolved significantly after the analysis window.

Neural Results

Neural analyses focused on the period between 100 and 500 ms following stimulus onset. This window was chosen a priori based on several considerations. The onset was chosen to allow Kalman filter predictions to stabilize, and to capture early evoked responses beginning with the N1/M100 auditory potential. The endpoint was chosen based on evidence from MEG, ERP and eyetracking results that show that sensitivity to manipulations of phonotactic frequency or neighborhood density for spoken words between 200 ms and 500 ms for visually presented (Pylkkänen et al., 2002; Stockall, Stringfellow, & Marantz, 2004) and auditorily presented words (Dufour et al., 2013; Hunter, 2013; MacGregor, Pulvermuller, van Casteren, & Shtyrov, 2012). We report all analyses related to the WORD and LOW ENTROPY NONWORD conditions here. The overall NONWORD condition (including both high and low entropy items) was also analyzed. However, because there is no independent evidence that this condition produces phonotactic frequency effects, these results are summarized here and presented fully in the supplementary materials.

We created different sets of regions of interest (ROIs) for trials including WORD versus NONWORD trials because lexicality emerged as a primary differentiator in behavioral performance measures. In addition, we created a set of ROIs² based on low entropy nonword trials because these trials produced significant behavioral evidence of phonotactic frequency effects, and behavioral effects that differed from those found in overall NONWORD trials in earlier work by Luce and Large (2001). ROIs were identified based on the MRI-constrained reconstructions of group averaged MEG/EEG activity in the 100–500 ms post stimulus onset period for both. These were labeled automatically by Freesurfer using the Desikan Killiany Atlas (Fischl, 2004). In all three conditions a number of regions in bilateral posterior lateral occipital cortex met the criteria for ROIs, but were excluded from the final ROI sets to facilitate computation, on the grounds that were likely related to low-level visual processes with no hypothesized connection to auditory language processing.

Twenty-three ROIs were subsequently identified in the WORD condition (Fig. 2 and Table 1). These included regions commonly implicated in spoken language processing including the left middle temporal gyrus (MTG), supramarginal gyrus (SMG), angular gyrus (AG), as well as right hemisphere superior temporal gyrus (STG), pars triangularis (PT) and bilateral inferior temporal gyrus and postcentral gyrus (postCG). Notably missing, were regions in the left STG, eliminated as potential ROIs due to redundancy with slightly more active right hemisphere homologs. This may reflect right hemisphere biases in MEG sensitivity to auditory cortex caused by cortical asymmetries (Shaw, Hamalainen, & Gutschalk, 2013). Given this redundancy, the results of Granger analyses involving right STG may also reflect left STG effective connectivity.

Automated analysis of the LOW ENTROPY NONWORD trials using the same parameters identified a set of 17 ROIs (see Fig. 3 and Table 2). These included ROIs in the left inferior temporal gyrus (ITG), left parahippocampal region (paraHip), post central gyrus (postCG), pre-central gyrus (preCG), pars opercularis (ParsOper), superior frontal gyrus (SFG), and superior parietal cortex (SPC). Right hemisphere ROIs included the supramarginal gyrus (SMG), superior temporal gyrus (STG) and pars triangularis (PT). As in the WORD condition, we found bilateral STG activation, but eliminated a potential left STG ROI due to redundancy with the timecourse of activation in the more strongly activated right hemisphere STG ROI. Multiple middle temporal gyrus (MTG) ROIs were found in both hemispheres.

Phonotactic Frequency Effects

Separate analyses were conducted for the WORD and LOW ENTROPY NONWORD conditions. With both sets, analyses of phonotactic frequency effects were limited to trials that involved low phonological neighborhood density items.

²NONWORD ROIs are described in the supplementary materials. Unlike the WORD and LOW ENTROPY NONWORD conditions, the NONWORD condition produced multiple distinct ROIs left and right STG. We hypothesize lexical feedback from a target word (WORD condition) or strongly activated competitor (LOW ENTROPY NONWORD) helps STG representations settle into a stable representation that is shared by bilateral STG. In the NONWORD condition, high entropy trials that produce no strong lexical candidates dilute this effect by allowing less constrained representations in bilateral STG to evolve more independently.

Granger analysis of the entire system showed a pattern of dense effective connectivity between ROIs in all conditions. For the purposes of hypothesis testing, we restricted our analyses to effective connectivity relationships involving the STG, a region implicated by pathology, electrophysiology and BOLD imaging in acoustic-phonetic processing (Boatman & Miglioretti, 2005; Hickok & Poeppel, 2007; Obleser & Eisner, 2009; Price, 2010). We hypothesized that any feedforward mechanism would involve mapping from STG to higher language areas, and any feedback effect would involve mapping from these areas back to STG.

In the WORD condition, there were no left STG ROIs. The right STG ROI that showed the strongest pattern of interactivity was the middle STG (R-STG2). The relative influences of right STG2 on other brain regions for high versus low phonotactic frequency words are shown in Fig. 4A. We found that six ROIs showed differential influence by right STG2 as a function of the phonotactic frequency of words. Binomial tests comparing the number of timepoints that show significant ($p < 0.05$) Granger Causation index values (GCI) showed stronger influence by right STG2 on activation in the right anterior inferior temporal gyrus (ITG) for high phonotactic frequency words, ($p < 0.05$). Right anterior ITG activation in linguistic tasks is typically associated with semantic processing (cf. Bookheimer, 2002; Price, 2012). In contrast, the influence of right STG2 for low phonotactic frequency words was higher on left SMG ($p < 0.0001$), left superior postcentral gyrus (postCG1) ($p < 0.001$), left inferior postCG2 ($p < 0.05$), right superior parietal cortex (SPC), ($p < 0.05$) and a more posterior portion of right STG (STG3) ($p < 0.0001$). As noted earlier the SMG, is associated with lexical processes and representation (Gow, 2012). The other regions are frequently activated in linguistic tasks, and are associated variously with somatosensory feedback (postcentral gyrus), high level auditory analysis (pSTG), and control processes in working memory (superior parietal cortex) (Hickok & Poeppel, 2007; Koenigs, Barbey, Postle, & Grafman, 2009; Price, 2012).

This result is inconsistent with the predictions of the feedforward account of phonotactic frequency effects, which suggested that high phonotactic frequency items should show a pattern of stronger influence by STG on activation in the lexically implicated SMG. If high phonotactic frequency items were more easily resolved at a prelexical level, or showed stronger weighting in the mapping from prelexical to lexical representation they should have produced stronger feedforward mapping. The fact that lower phonotactic frequency words showed stronger STG influence on SMG activation may be due to the distinctiveness of low phonotactic frequency words from sparse neighborhoods. Such items should be easily distinguished from lexical competitors. Few competitors should receive partial activation, and so competition effects should have little influence on the activation of the target word.

The relative influences of other ROIs on right middle STG for high versus low phonotactic frequency words are shown in Fig. 4B. As predicted by the lexical mediation hypothesis, high phonotactic frequency words produced stronger influence by lexical regions on activation in the prelexical STG. In these comparisons, all significant phonotactic frequency effects favored high frequency words. High phonotactic frequency words produced stronger influences by left SMG2 ($p < 0.01$), left SMG1 ($p < 0.05$), right SMG ($p < 0.005$) and right ITG2 ($p < 0.001$). While converging evidence from BOLD imaging, anatomy, and pathology

primarily implicate left SMG in lexical representation (Gow, 2012), Hartwigsen et al. (2010) have shown that disruption of right SMG function impairs judgments of syllable number. Syllable number is a property of whole words, and so this result raises the possibility that right SMG may also play a role in lexical representation. None of the areas that showed different levels of influence on STG2 activation as a function of phonotactic frequency manipulations has been implicated in response selection in linguistic tasks.

Evidence from behavioral competition effects (c.f. Allopenna et al., 1998; Marslen-Wilson, 1990; Spivey, Grosjean, & Knoblich, 2005), and fragment priming (Marslen-Wilson & Zwitserlood, 1989) demonstrate that word recognition involves some parallel activation of lexical candidates with overlapping phonological patterns. Prabhakaran et al.'s BOLD imaging results (2006) suggest that this is indexed by left SMG activation in auditory lexical decision. The current results suggest that this cohort of partially activated lexical candidates influences acoustic-phonetic activation. This interpretation is consistent with the finding that SMG influences on STG activation produce a perceptual bias towards interpreting phonemes in nonword contexts in a way that favors lexically attested phonotactic patterns (Gow & Nied, 2014). It is also consistent with Newman et al.'s finding that neighborhood density influences categorization judgments about ambiguous phonemes heard in nonword contexts (1997).

Analyses of phonotactic effects involving all NONWORD trials (supplementary materials) showed generally stronger feedforward influences by bilateral STG for low phonotactic frequency items, but no significant effects of phonotactic frequency in mapping from any STG ROI to lexically implicated SMG or MTG ROIs. Phonotactic frequency manipulations had no effect on the strength of influence by these lexical ROIs on either STG ROI. This lack of phonotactic frequency effects in mapping between lexical and acoustic areas is consistent with the lack of behavioral evidence for phonotactic effects for these stimuli in behavioral work (Luce & Large, 2001).

Comparisons of Granger effects between high and low phonotactic frequency LOW ENTROPY NONWORDS were all made in reference to the right STG ROI (Fig. 5). Binomial tests showed stronger feedforward effects for high phonotactic frequency nonwords by the right STG on left SFG2 ($p < 0.05$), left preCG, ($p < 0.05$), and right MTG2 ($p < 0.01$). Lower phonotactic frequency nonwords produced stronger feedforward effects from right STG on left MTG1 ($p < 0.025$), Left MTG3 ($p < 0.05$), and right MTG1 ($p < 0.01$).

Like the WORD and NONWORD analyses, LOW ENTROPY NONWORD analyses did not find stronger feedforward influence from acoustic phonetic representation in STG to lexical areas by higher phonotactic frequency items (Fig 5A). Posterior MTG activation is associated with lexical representation (Gow, 2012; Hickok & Poeppel, 2007), but the right MTG2 is considerably anterior to these regions. As in the WORD condition, low phonotactic frequency items produced stronger feedforward influences on lexically implicated bilateral posterior MTG (left MTG3 and right MTG2).

Comparisons of top-down influences on right STG activation show stronger influences in the high phonotactic frequency condition by left SFG1 ($p < 0.01$), left SFG2 ($p < 0.001$), and right SMG ($p < 0.01$). Top-down influences on right STG activation were stronger for low phonotactic frequency nonwords for left MTG2 ($p < 0.001$), left paraHip ($p < 0.05$), right MTG1 ($p < 0.001$), and right MTG2 ($p < 0.001$) (Fig. 5B). The SFG and parahippocampus play a role in both working memory and semantic processing (Binder, Desai, Graves, & Conant, 2009; Meda, Stevens, Folley, Calhoun, & Pearlson, 2009). In the processing of low entropy nonwords, this role may be related to the maintenance (or perhaps suppression) of wordforms that closely resemble, but mismatch the target items.

The pattern of top-down influences on STG activation for low entropy nonwords resembles that shown by words. As in the WORD condition, higher phonotactic frequency items produced stronger influences by SMG, another region implicated in lexical representation (Gow, 2012; Hartwigsen et al., 2010). However, while acoustic-phonetic processing in STG was influenced by both left and right SMG in words, low entropy nonwords produced only a right SMG effect. There was also a reversed top-down effect, with low phonotactic frequency nonwords showing strong top influences on STG by lexically implicated right posterior MTG (right MTG1). These items may closely approximate, but clearly fail to match a word.

Implications

The goal of this work was to isolate and characterize the mechanisms that produce phonotactic frequency effects in spoken word recognition. Our results suggest that high phonotactic frequency words benefit from a classic perceptual “gang effect” (McClelland & Rumelhart, 1981) in which stored lexical representations facilitate acoustic-phonetic processing of words with overlapping phonotactic patterns. This advantage is multiplied in the perception of words that overlap with many stored representations.

The finding that low phonotactic frequency words show stronger feedforward mapping from STG to SMG than higher phonotactic frequency words directly contradicts the predictions of a feedforward account of phonotactic frequency effects. It suggests that, at least for auditory lexical decision, there is no feedforward advantage in the processing of high phonotactic frequency items. Moreover, the significant reversal of the predicted feedforward advantage demonstrates that our results cannot be attributed to a lack of sensitivity in our measures. This finding is inconsistent with the suggestion that phonotactic frequency biases provide a feedforward explanation for lexical influences on speech perception (Cairns et al., 1995; McQueen, 2003; McQueen et al., 2009; Pitt & McQueen, 1998). This does not rule out the possibility that feedforward mechanisms also contribute to phonotactic frequency effects. However, if they do, they do so either in early (precortical) mapping, or through within-ROI dynamics that are not captured by our analyses.

Why then do we find stronger feedforward effects for low phonotactic frequency items? Feedforward Granger causation from acoustic-phonetic to lexical brain regions indexes the ability of patterns of activation reflecting acoustic-phonetic representation to resolve patterns of activation reflecting lexical activation. Concretely, resolution may be roughly thought of as a measure of how many lexical candidates are partially activated. Strong

resolution (or Granger causation) should mean the partial activation of fewer candidates. Low phonotactic frequency items overlap with fewer lexical candidates and so provide more resolution. It is notable that other work has shown that high phonotactic frequency words and nonwords (from large neighborhoods) produce stronger activation than their lower phonotactic frequency counterparts in lexical decision as indexed by the amplitude of the P2 component (240–300 ms) (Hunter, 2013). Significantly, they also produce stronger activation as a function of the frequency of the initial phoneme from 127–163 ms post stimulus onset, before lexical neighborhood effects become a factor. Here, stronger activation may reflect the partial activation of a larger set of overlapping lexical candidates. This reversal of effects underscores the dissociation between measures of overall activation and Granger causality.

One unexpected finding was a difference in the source of lexical influences on acoustic-phonetic processing in the word versus low-entropy nonword conditions. In the WORD condition, lexical effects took the form of Granger influence by SMG on STG. In the LOW ENTROPY NONWORD condition they involved influence by the MTG on STG. The dual lexicon model (Gow, 2012) provides a framework for understanding the differing roles of SMG and MTG in lexical processing. Based on synthesis of evidence from dissociations between different types of lexical effects in behavioral results, aphasia and BOLD imaging, the dual lexicon model suggests that lexical representations in these areas act as hidden nodes, facilitating the mapping between acoustic-phonetic representations in STG and processing within the dorsal and ventral speech streams described by Hickok and Poeppel (2004, 2007). In this model, a dorsal lexicon (SMG) mediates the mapping from acoustic-phonetics to articulation, and a ventral lexicon (MTG) mediates the mapping from acoustic-phonetics to meaning. Both regions have been shown to play a role in lexical effects on speech processing (Gow & Nied, 2014; Gow & Segawa, 2009; Gow et al., 2008). Based on the pattern of stronger feedforward influences of STG on SMG for both high low-phonotactic frequency words and low entropy nonwords, we hypothesize that failure to map with lexical representations in the SMG-based dorsal lexicon may trigger secondary analyses involving the observed reciprocal interactions between this middle temporal ventral lexicon and STG during the processing of low-entropy nonwords.

Future work will be needed to model the ways factors such as lexically mediated compensation for coarticulation, perceptual learning, post-perceptual decision biases and others combine with top-down lexical influences on speech perception to shape phoneme perception and categorization in citation form and connected speech.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Appendix. High versus low phonotactic frequency words and nonwords.

Low entropy nonwords are indicated by an asterisk

Word		Nonword	
High	Low	High	Low
beam	beg	ba m	bep*
bib	book	b v*	dæd *
bob	cave	bæv*	dæt
bomb	check	dab	dUs
con	chef	dap	f g*
dawn	chill	d p*	f d
deaf	choke	d v*	f s
dock	dish	dæl	ga s
doll	fish	fa k*	h
dose	foot	fam	h

Word		Nonword	
High	Low	High	Low
fern	full	f p	h n*
fig	geese	fim*	h p
foam	gone	fæp*	hus
folk	half	fæv	kit
fuss	hedge	fos	log*
gas	hoop	g s	lUn
guess	hope	ham*	lov*
hearse	howl	h b	l 's
hem	laugh	hos*	ma v
hen	lawn	h s	m aUl*
hire	leg	kob*	m
home	lobe	lam*	miv
kiss	luce	lan*	mæŋ
knock	match	l p*	mum*
learn	mesh	læl	na r*
limb	mood	lær	num*
live	niece	mim	pat *
lull	noon	mæb*	p z*
mob	null	mæv*	ra b*
mop	path	mom*	r *
mud	pave	n m	ro *
myth	phase	n s	ruk
neck	pout	næs*	r z
palm	pull	pab	m
peck	ridge	p m*	sæθ*
pope	ripe	pæv	om*
purse	roach	p 'd	'n
rib	rug	ral*	sud *
sour	safe	r v*	su l
tab	shine	ræv	tæd
tar	ship	s v	t m*
tip	shown	t d*	t in
top	tape	tæv*	t æs*
van	taut	tos*	t os*
wreck	wrath	væs	vit*

Highlights

- We tracked brain activity during auditory LD manipulating phonotactic frequency.
- We measured effective (directed) connectivity between brain regions.
- Low frequency items had stronger feedforward mapping from speech to word areas.
- High frequency items produced stronger top-down mapping from word to speech areas.

Fig. 1.
Behavioral results for lexical decision task by accuracy.

Fig. 2. Regions of interest identified in the WORD condition. Numbers indicate the rank of mean activation strength in each parcellation unit in units with more than one ROI.

Fig 3. Regions of interest identified for low entropy items in the NONWORD condition. Numbers indicate the rank of mean activation strength in each parcellation unit in units with more than one ROI.

Fig 4.

Relative causation strength (difference in number of time points that show GCi values with $p < 0.05$) for high versus low frequency WORDS showing all differences with $p < 0.05$. Circle diameter indexes effect size. Panel A shows relative bottom-up influences from right STG2 on other ROIs. Panel B shows relative top-down influences of other ROIs on right STG2 activation.

Fig 5.

Relative causation strength (difference in number of time points that show GCi values with $p < 0.05$) for high versus low frequency LOW ENTROPY NONWORDS showing all differences with $p < 0.05$. Circle diameter indexes effect size. Panel A shows relative bottom-up influences from right STG on other ROIs. Panel B shows relative top-down influences of other ROIs on right STG activation.

Table 1

Regions of interest and MNI coordinates of their vertices showing the strongest mean activation (100–500 ms) in group-averaged data in the WORD condition.

ROI	Location MNI	Coordinates (X, Y, Y)		
Left				
AG 1	Angular gyrus	−38.94	−86.15	24.7
ITG 1	Inferior temporal gyrus	−57.29	−39.04	−28.64
MTG 1	Middle frontal gyrus	−68.38	−24.72	−12.86
SFG 1	Superior Frontal gyrus	−13.39	−0.23	72.29
SMG 1	Supramarginal gyrus	−64.96	−32.8	33.63
SMG 2	Supramarginal gyrus	−53.11	−47.9	48.25
postCG 1	Postcentral gyrus	−10.56	−40.95	77.23
postCG 2	Postcentral gyrus	−62.29	−10.11	35.84
preCG 1	Precentral gyrus	−54.8	−5.95	48.41
Right				
Fusi 1	Fusiform gyrus	40.85	−73.05	−18.04
ITG 1	Inferior temporal gyrus	58.75	−33.76	−27.97
ITG 2	Inferior temporal gyrus	57.39	−19.94	−36.83
ParaHip 1	Parahippocampus	9.5	−90.35	−13.2
ParsTri 1	Pars triangularis	50.67	28.98	14.96
SMG 1	Supramarginal gyrus	63.78	−41.59	27.76
SPC 1	Superior Parietal cortex	11.13	−50.75	73.15
STG 1	Superior temporal gyrus	66.78	−25.65	7.94
STG 2	Superior temporal gyrus	66.32	−14.72	5.65
STG 3	Superior temporal gyrus	65.57	−31.74	15.53
STS 1	Superior Temporal Sulcus	62.22	−42.94	13.72
postCG 1	Postcentral gyrus	65.45	−7.83	9.54
postCG 2	Postcentral gyrus	55.6	−10.49	38.14
preCG 1	Precentral gyrus	23.79	−19.39	73.3

Table 2

Regions of interest and MNI coordinates of their vertices showing the strongest mean activation (100–500 ms) in group-averaged data in LOW ENTROPY NONWORD condition.

ROI	Location MNI	Coordinates (X, Y, Y)		
Left				
ITG 1	Inferior temporal gyrus	−50	−59.92	−13.04
MTG 1	Middle frontal gyrus	−68.38	−24.72	−12.86
MTG 2	Middle frontal gyrus	−62.83	−6.76	−24.5
MTG 3	Middle frontal gyrus	−64.06	−56.34	3.88
ParaHip 1	Parahippocampus	−10.32	−85.16	−15.38
ParsOper 1	Pars opercularis	−54.35	26.23	13.89
SFG 1	Superior Frontal gyrus	−4.27	12.04	57.9
SFG 2	Superior Frontal gyrus	−17.36	−7.09	70.7
SFG 3	Superior Frontal gyrus	−8.79	59.67	32.2
SPC 1	Superior Parietal cortex	−19.13	−84.98	40.71
postCG 1	Postcentral gyrus	−14.36	−41.56	77.56
preCG 1	Precentral gyrus	−5.89	−23.84	76.09
Right				
MTG 1	Middle frontal gyrus	66.27	−49.95	0.06
MTG 2	Middle frontal gyrus	59.44	−13.72	−27.36
ParsTri 1	Pars triangularis	56.55	21.34	10.44
SMG 1	Supramarginal gyrus	61.7	−44.11	15.46
STG 1	Superior temporal gyrus	63.23	−14.14	5.91