Shared early pathways of word and pseudoword processing: Evidence from high-density electrocorticography

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1 Introduction

In psycholinguistic studies of lexical processing, language users' responses to real words are often compared to novel pseudoword forms. The goal of these comparisons is to learn something about the architecture of the lexical processing system, by examining or inferring the processing pathways evoked by words, which have full phonological, lexical, grammatical, and semantic representations. These are compared to pseudowords, which are assumed to lack all linguistic information at levels higher than the phonological representation, due to their novel status. However, the precise nature of pseudoword representation is still a subject of inquiry, one that is critical to understanding precisely what is being isolated in the lexical processing system in experiments where words and pseudowords are compared. The present study contributes to this line of research by providing data on the neural processing of words and pseudowords in an auditory listening task.

2 Previous research

2.1 Theories of pseudoword processing streams

In studies of word reading, models of processing have been proposed in which words and pseudowords employ different processing pathways, one facilitated by sublexical processes and the other by lexical processes (Coltheart et al. 1993, 2001, see also Marshall and Newcombe 1973). This argument, the dual-route theory, is built upon the observation that readers with different types of dyslexia may or may not be impaired when reading pseudowords, a distinction ascribed to whether or not the sublexical (phonological) level of processing is impaired. Although designed to explain processing with visual presentation of stimuli, this theory has been extended to examine word and pseduworod proccessing in the auditory domain as well (Glosser et al. 1998), making it a more general account of the distinction between novel forms and stored lexical representations. However, on another account, pseudowords and words utilize shared processing pathways, with processing differences attributable to different degrees of engagement of various components of the system. An argument in the connectionist tradition (e.g. Seidenberg and McClelland 1989) argues against the dual-route theory by positing that differences between words and pseudowords reflect differences in how strongly orthography, phonology, and semantics are activated, but not to entirely different

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processing pathways.

Many studies implicitly or explicitly adopt the latter position, and presume shared early pathways for words and pseudowords. More specifically, the position taken by many experimental studies using pseudowords as auditory stimuli is that pseudoword processing engages only the earliest stages of this pathway (e.g. Tavabi et al. 2009, Acherson et al. 2011). Under this assumption, pseudowords are processed at auditory and phonological levels, but due to their novel status, have no content to be processed at higher-level (lexical, grammatical, or semantic) components of the system. For this reason, they are often considered to be ideal controls to contrast with real words; under this assumption, any evidence of processing for words that does not occur with pseudowords should be indicative of these higher processing levels.

However, this position - whether explicitly stated or implicitly assumed in the design of an experimental task - may over-simplify the nature of pseudoword representation. Pseudowords can be constructed so as to be decomposable into morphological subcomponents (Deacon and Kirby 2004), and the degree to which they are decomposable has been shown to affect how they are processed (Caramazza, Laudanna, and Romani 1988). Furthermore, Price et al. (1996) demonstrated that although pseudowords do not have stored lexical representations, they activate a similar network of brain regions as words do, even in regions which are taken to represent lexical or semantic levels of processing. This result is consistent with the idea that novel forms instigate an effortful "search" for representations in higher processing levels. Such a search ultimately fails due to the unavailability of any representations matching their phonological content, but it nevertheless indicates that processing of pseudowords may not be restricted to auditory and phonological levels.

Because pseudowords are ubiquitous in studies which examine the architecture of language comprehension, it is critical to be precise about the levels of processing that we expect them to engage in order properly interpret experimental results. Specifically, it is important to know: (1) Do words and pseudowords share processing pathways in early levels of processing, or do they quickly diverge along lexical-sublexical routes? (2) Do pseudowords engage only "sound-based" (auditory, orthographic, phonetic, and/or phonological) levels of processing, or are higher-level (lexical, grammatical, semantic) stages engaged in some way as well?

2.2 Evidence from neuroimaging

Recently, studies on the neural processing of pseudoword stimuli have attempted to clarify the nature of their representations. Ideally, these methodologies hold the promise of distinguishing between possible theories of processing pathways, as they highlight which functional regions are engaged when processing a stimulus, and the sequencing of these responses along a neural pathway. The ability to measure neural activity and its physiological correlates allows neuroimaging tasks to take advantage of passive listening paradigms, which reduce confounding factors in processing or attention attributable to over behavioral responses. The replication of behavioral paradigms such as lexical decision tasks (Raettig and Kotz 2008, Hauk et al. 2006) and repetition procedures (Orfanidou et al. 2006, Glosser et al. 1998) are also used to complement results from behavioral studies.

But despite the promise of the medium, the assembled literature of neuroimaging studies comparing word and pseudoword processing to date is inconclusive, with poor agreement about critical regions of precessing, temporal sequencing of processing stages, and the comparative magnitude of neural responses to the two types of stimuli. Mechelli and colleagues (2003) identify several methodological and theoretical challenges which ave impeded a unified set of results; in particular, a lack of clear predictions at the neural level by theoretical models makes explicit testing of predictions difficult, and the enhancement of individual differences as a function of small subject pools may magnify inconsistencies between studies. Raettig and Kotz (2008) review a series of findings and note that some studies fail to distinguish activation patterns for words and pseudowords at all, while others do. Of the latter group, there is a split between those who show heightened activity for words, heightened activity for pseudowords, or both patterns in different regions. They do note some cross-study consistency in regions which show enhanced activation for real words (left/bilateral middle and inferior temporal areas, areas around the temporo-parietal junction), but no similar set of regions emerges for heightened pseudoword activation. They attribute study inconsistencies to the composition of pseudoword stimuli, which can vary on their phonological content and similarity to real words.

With respect to the hypotheses outlined above, some neuroimaging studies have found that pseudowords utilize the same processing pathways as real words (e.g. Glosser et al. 1998). Furthermore, many of these studies show responses to pseudowords in areas believed to play a role in lexical or semantic processing stages, suggesting that pseudoword processing is not exclusively auditory/phonological processing (Price et al. 1996, Mechelli et al. 2003). Several of these studies (Hauk et al. 2006, Newman and Twieg 2001, Raettig and Kotz 2008, Xiao et al. 2005) show heightened activation for pseudowords over words, suggesting that novel forms require more effortful processing than comparably familiar real words. However, there is also neuroimaging work consistent with the dual-route theory in reading paradigms (Jobard et al. 2003, Heim et al. 2005); less work has tested this theory in auditory pseudoword/word processing. Thus, even within studies that make clear predictions, the nature of pseudoword processing pathways remains an open question.

2.2.1 Studies using intracranial recording techniques

To date, a handful of studies have compared word and pseudoword processing using intracranial recording techniques. These methodologies are used to record activity directly off the cerebral cortex or at sub-cortical regions using either a gridded network of electrodes, as in electrocorticography, or at deeper cortical structures, using depth electrodes. Participants in these studies are patients who are candidates for neurological surgery. Grid or electrode placement is determined by patients' clinical needs, but often provides sufficient coverage of the temporal, frontal, and parietal lobes to gather information about linguistic processing. The advantage of these techniques is a finer resolution of spatial and temporal information than is typically available in conventional neuroimaging techniques, as well as an ability to integrate the two dimensions in a way that is not usually available to studies measuring hemodynamic responses or scalp-level electrical or magnetic activity. These invasive techniques may help to resolve some of the debate about lexical and pseudoword processing pathways, as the flow of information from one brain region to another, corresponding to the stages or pathways of processing, are more clearly observable.

Tanji et al. (2005) examined high-gamma activity in response to visually-presented Japanese words and pseudowords in a lexical decision task. Stimuli were presented as both kanji (logo/morphographic) and kana (syllabic) wordforms. The authors found heightened responses to pseudowords over words, in line with several previous studies which suggest a greater effort for processing pseudowords. However, the difference only applied to kanji wordforms, which may have reflected extra effort required to instantiate a phonological representation from an unfamiliar logographic form. Gow et al. (2009) measured pathways of auditory processing in response to word, pseudoword, and ambiguous stimuli. They found comparable patterns of activity for word and pseudoword stimuli, particularly in sites along in the temporal lobe, originating in the pSTG and flowing in an anterior direction., They attribute this result to processing along the ventral stream (Hickok and Poeppel 2004, 2007, Scott and Wise 2004), the pathway which maps sound to meaning.

Mainy et al. (2008) examined the regions of the cortex associated with visual word recognition and dissociation between word and word-like stimuli with different lexical properties. Their results suggest that word and pseudowords may ultimately dissociate in Broca's area, with responses to visually presented stimuli showing activity consistent with semantic processing in the anterior part of the region (pars triangularis) and phonological or grapheme-to-phoneme conversion in the posterior region (pars opercularis). Simultaneous activity in the STG did not differentiate words and pseudowords. Their paradigm did not use tasks that directly compared words and pseudowords, and as such their contrasts should be interpreted cautiously, but their results demonstrated that intracranial recordings are a promising avenue for disentangling lexical processing pathways.

The current study expands upon this work, by exploring auditory lexical processing with electrocorticography during auditory presentation of words and pseudowords. It specifically focuses on early stages of processing, by examining pathways engaged in the temporal lobe during listening/comprehension. The expectation is that it will be possible to observe activity along pathways from early processing in the posterior superior temporal gyrus (pSTG) through processing to the middle temporal gyrus (MTG), anterior superior temporal gyrus (aSTG), and superior temporal sulcus (STS). According to models by Hickok and Poeppel (2004, 2007) and Scott and Wise (2004), early processing in the pSTG reflects initial auditory/phonetic processing; from there, processing diverges into a ventral stream down the anterior length of the temporal lobe, where a sound-to-meaning mapping on the one hand, and to the superior temporal sulcus on the other, where a pathway called the dorsal stream is formed linking phonetic to articulatory information. These pathways can be mapped on to traditional linguistic models of phonological, lexical, and semantic pathways, and provide predictions on where different stages of processing should be located.

If word and pseudoword processing use divergent lexical and sublexical processing streams during early listening/comprehension, it is predicted that patterns of activity should show strongly different responses early after stimulus presentation - either through the activation of different populations of electrodes, or through strongly attenuated responses in shared channels depending on trial type. If, however, they share early processing mechanisms, then the same electrodes should show activity within a comparable level of magnitude for words and pseudowords. If this is the case, we may see the restriction of this shared pathway to the dorsal stream for pseudowords, suggesting that lexical level processing is reserved for real words. Alternately, pseudowords may show activity similar to real words in early ventral stream processing, suggesting an attempt to interface to higher-level lexical/semantic information.

3 Methods

3.1 Subjects

Three individuals participated in this study. All subjects were patients who had undergone a surgical procedure to implant a high-density (256-channel) electrode array on the cerebral cortex of the left hemisphere, with 4 mm spacing between each electrode. Grid placement was a reflection of the patient's specific clinical needs. Grid placement maps are provided in Appendix B. The study was conducted in extraoperative experimental sessions at the University of California, San Francisco Medical Center.

3.1.1 Stimuli and procedure

The current analysis examines neural responses to auditorily-presented words and pseudowords. This data was taken from a larger task involving a repetition paradigm, where patients were required to repeat each stimulus after they heard it. Analyses presented below consist of neural responses during the first one second of each trial in this task, from the onset of the auditory stimulus to approximately 150 milliseconds (on average) after the stimulus offset. This window was selected to examine processing during and immediately after listening, while excluding the time during which participants prepared an articulatory routine and spoke.

The stimulus set of the current study consisted of ten real words and ten pseudowords. The ten words in this analysis were drawn from the larger task's set of 35 real words, and were selected because they closely matched the phonological and segmental composition of the pseudowords. Specifically, the pseudowords were created on the basis of this set of ten words, by switching the position of two syllables in a real word (e.g. "repetition" → "pitereton"). Thus, each word had a closely-matched pseudoword form. Both words and pseudowords in the present analysis were four syllables long, comprised of syllables with consonant-vowel or consonant-vowel-consonant structures.

3.1.2 Data processing

Neural data was recorded in 256 electrode channels; of these, a subset in each patient was selected for analysis which consisted of all electrodes in the temporal lobe, identified as those which fell below or at the Sylvian fissure. The data was recorded at a sampling rate of 3050 Hz, and downsampled to 400 Hz for analysis. All data was visually inspected to remove artifacts and noisy channels. Electrical line noise and other cross-channel aberrations were removed by subtracting the common average reference (a mean across time points, within blocks of 16 channels) from the raw data. Data from the high-gamma (70-150 Hz) frequency band was selected for analysis. High-gamma has a high signal-to-noise ratio and is thought to be a reliable index for neuronal activity in tasks across a range of functions and modalities, including linguistic tasks (Crone et al. 2001, Edwards et al. 2005, Canolty et al. 2007, Flinker et al. 2011, Chang et al. 2011). These preprocessing procedures were implemented with custom MATLAB scripts written in the Chang Lab at UCSF. In all analyses presented below, normalized power values averaged over the high-gamma band are presented as a z-score compared to baseline activation. This baseline was sampled from a quiet resting phase at the end of each experimental block.

4 Results

4.1 Identification of significant temporal lobe activity

For each patient, electrodes which lay at or below the Sylvian fissure were identified for analysis. This totalled 101 electrodes for patient 1, 105 for patient 2, and 122 for patient 3. Each electrode was assessed for significant activity by comparing its average activity over the 1-second window to a baseline value of zero using a one-sample t-test. Each comparison was assessed at an adjusted level of $p < 0.05$ using a false discovery rate (FDR) correction for multiple comparisons (after Canolty et al. 2007, Flinker et al. 2011), with the corrections level set by the number of electrodes identified in the temporal lobe for each patient. This comparison yielded 93 significantly active electrodes for patient 1, 104 electrodes for patient 2, and 112 electrodes for patient 3. This indicated that much of the length of the temporal lobe which was covered in each patient was significantly involved in processing during and immediately after the presentation of the experimental stimuli.

Activation along the span of the temporal lobe is not predicted to be uniform. In the dorsal/ventral stream model of auditory linguistic processing, portions of the superior temporal gyrus (STG) are predicted to involve phonetic and phonological processing, while the middle temporal gyrus (MTG) is proposed to involve lexical and semantic processing (Hickok and Poeppel 2007). Thus, in the current study, electrodes were grouped into two sets: those that fell along the superior temporal gyrus, and those that fell inferior to the superior temporal sulcus - primarily on the middle temporal gyrus (although some grid coverage extended partially into the inferior temporal gyrus as well). Further analyses were conducted separately on the two anatomical groups for each patient, in order to examine the degree to which their functional activity differed.

4.2 Word/pseudoword differences over the duration of the trial

Activity over the time course of the trial was examined in broad STG and MTG groups in each patient, to determine if differences between word and pseudoword processing existed, and whether those differences were manifested equally over the trial, or whether activity levels were shared at certain time points and diverged at others. Activity was sampled in 50-millisecond epochs over the course of the one-second analysis window, giving 20 average values for the activity in a given electrode. Linear models were constructed for each region (STG or MTG) in each of the three patients. The details of these models are shown in table 4.2. Average activation patterns over the course of the trial for each patient and region are shown in figure 1.

Table 1: Details of the linear models assessing the effect of trial type and time on average activity for each patient and brain region (activity as a function of time by trial type).

Patient	Brain region	F-stat (df)	Model R^2	model p-value	p-value, time	p-value, trial type	p-value, time * trial type
1	STG	87.71 (df = 39, 90400)	0.036	$p < 0.00001$	$p < 0.00001$	$p < 0.00001$	$p = 0.00025$
1	MTG	30.73 (df = 39, 50880)	0.022	$p < 0.00001$	$p < 0.00001$	$p < 0.00001$	$p < 0.00001$
2	STG	281.6 (df = 33, 84575)	0.099	$p < 0.00001$	$p < 0.00001$	$p < 0.00001$	$p < 0.00001$
2	MTG	45.01 (df = 33, 56372)	0.025	$p < 0.00001$	$p < 0.00001$	$p < 0.00001$	$p < 0.00001$
3	STG	294.7 (df = 39, 159420)	0.067	$p < 0.00001$	$p < 0.00001$	$p < 0.00001$	$p < 0.00001$
3	MTG	64.12 (df = 39, 103900)	0.023	$p < 0.00001$	$p < 0.00001$	$p < 0.00001$	$p < 0.00001$

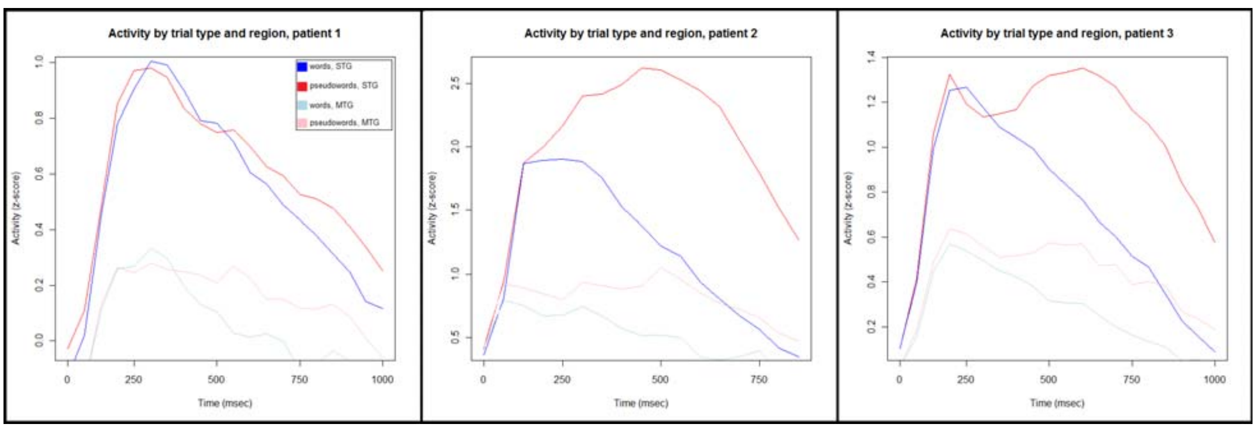

Figure 1: Average activity for word and pseudoword trials in the STG and MTG

From visual inspection of the data, two patterns are apparent. First, activity in the STG electrodes, as a whole, are much stronger than in the MTG electrodes. In addition, it appears that across patients and brain regions, activity in response to pseudowords and words starts off with similar latencies and magnitude, including comparable latencies of peak activation. However, in both the superior and middle temporal gyri, activation continues at a higher magnitude and a more sustained latency in response to pseudoword as opposed to word stimuli.

The latency differences are partly attributable to the longer average duration of pseudoword stimuli as compared to word stimuli (average pseudoword duration = 837 milliseconds, sd = 62; average word duration = 769 milliseconds, sd = 66; Wilcox rank-sum test, W = 358, $p < 0.0001$). However, the difference between the latencies of sustained activation for words and pseudowords appears to be greater than the mean difference (67 milliseconds) of the duration of the two trial types; furthermore, the activation patterns differ in magnitude as well as latency, with greater activity for pseudowords over words.

Table 2: Details of the linear models assessing the effect of trial type and electrode on average activity for each patient and brain region (activity as a function of electrode by trial type).

Patient	Brain region	F-stat (df)	Model R^2	model p-value	p-value, time	p-value, trial type	p-value, electrode * trial type
Patient 1	STG	295.3 (df = 119, 90320)	0.279	$p < 0.00001$	$p < 0.00001$	$p < 0.00001$	$p < 0.00001$
Patient 1	MTG	95.09 (df = 67, 50852)	0.110	p ¡ 0.00001	$p < 0.00001$	$p < 0.00001$	$p < 0.00001$
Patient 2	STG	366.3 (df = 125, 84483)	0.351	$p < 0.00001$	$p < 0.00001$	$p < 0.00001$	$p < 0.00001$
Patient 2	MTG	183.9 (df = 83, 56322)	0.212	$p < 0.00001$	$p < 0.00001$	$p < 0.00001$	$p < 0.00001$
Patient 3	STG	367.3 (df = 133, 159326)	0.182	$p < 0.00001$	$p < 0.00001$	$p < 0.00001$	$p < 0.00001$
Patient 3	MTG	284.7 (df = 89, 103850)	0.195	$p < 0.00001$	$p < 0.00001$	$p < 0.00001$	$p < 0.00001$

Time-locked differences were examined at a finer-grained level with post-hoc comparisons (using Tukey's honestly significant difference test, adjusted $p < 0.05$) of the differences in activity in response to words and pseudowords at each 50-millisecond window. In all patients and both brain regions, these comparisons were significant primarily in the later part of the trial. In the superior temporal gyrus, the word-pseudoword comparison was different for patient 1 at 925 milliseconds after trial onset, for patient 2 at 125 msec post-onset and then from 375 msec to the end of the window, and for patient 3 from 425 msec post-onset through the end of the window. In the middle temporal gyrus, comparisons reached significance for patient 1 at 525, 575, 725, 775, 825, and 925 milliseconds post-onset, and for patients 2 and 3, from 425 milliseconds post-onset through the end of the window. In all cases, significant comparisons indicated greater activity in response to pseudowords over words. These comparisons should be interpreted cautiously, as they do not correct for correlations between successive time points; however, as a general trend they suggest an increasing separation between activity in response to pseudoword and word stimuli as listening unfolds.

4.3 Spatial differentiation of lexical patterns

In order to examine the spatial distribution of lexical differences, further analyses were carried out to examine which temporal lobe electrodes reflected processing differences between words and pseudowords. As in the temporal analysis, a linear model was fit to the STG and MTG regions in each patient, averaged across time. These analyses are summarized in table 4.3.

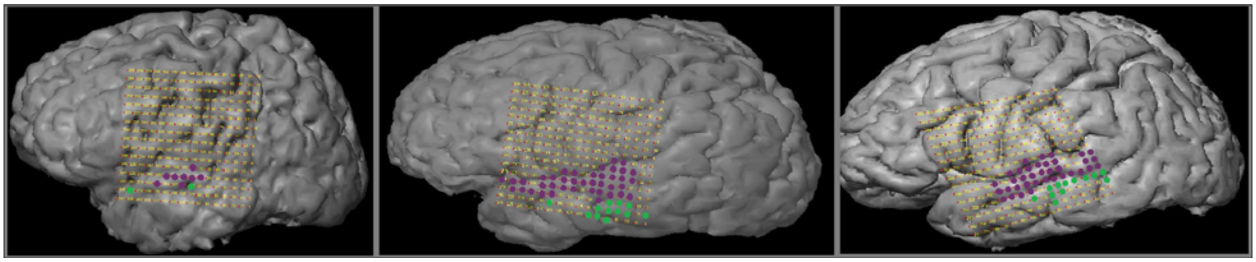

Figure 2: Electrodes showing a significant difference between words and pseudowords, patient 1 (left), patient 2 (center), and patient 3 (right). Electrodes in purple are those identified in the STG; green electrodes are those identified as being in the MTG.

Figure 2 shows the distribution of electrodes in each patient which showed a significant contrast in the magnitude of activity in response to words and pseudowords (Tukey's post-hoc correction, adjusted $p < 0.05$). No electrodes were selectively active in any patient for either words or pseudowords, but several did show differences in the magnitude of activity between the two trial types - in all cases, with more activity for pseudowords than words.

The location of electrodes which showed a significant difference varied somewhat between patients. In patient 1, differences between words and pseudowords are confined to the middle and anterior regions of the temporal lobe, primarily in the STG. This concentration is also found in patient 2, but with more posterior electrodes showing a distinction as well. Patient 3 has a broad distribution, from relatively posterior electrodes to the farthest anterior temporal lobe position on the grid. Electrodes showing a lexical difference across patients in the MTG are nearly exclusively in the posterior and mid-regions, and lie closely along the superior temporal sulcus.

4.4 Examination of possible acoustic differences

A concern with the analyses presented above is that the differences may not be attributable to the lexical status of the stimuli, but rather a function of the tuning properties of the auditory cortex. There is finely-localized cortical specificity in the human auditory cortex to detailed spectrotemporal information in the acoustics of speech sounds (Bitterman et al. 2008, Talavange et al. 2004). As a result, it is possible that the demonstrated differences between words and pseudowords may be an artifact of acoustic tuning - perhaps more electrodes are tuned to the types of acoustic features that are more prevalent in the pseudoword stimuli. Although the construction of the pseudowords was designed to match their real word counterparts in syllable structure and segmental content as closely as possible, it cannot be assumed that this would translate to an identical acoustic-neural representation. It is possible, for example, that initial segments are more critical to recognition than segments later in a word, and thus an asymmetry could be introduced by the simple ordering of segments in the pseudowords as compared to the words in the data set.

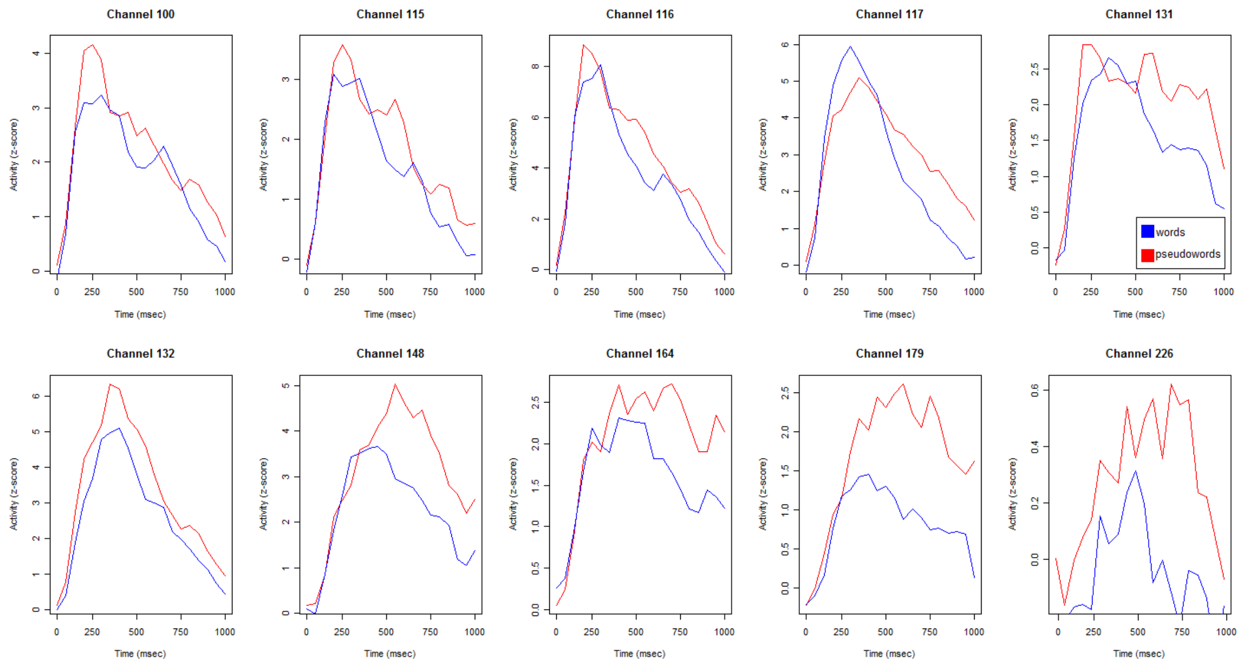

Figure 3: Average activity for word and pseudoword trials for electrodes in patient 1 which showed a significant channel * trial type interaction

To explore whether differences are more likely to be a function of acoustics or lexical properties, this section looks at data from patient 1 in more detail. Figure 3 shows activation for the ten electrodes from patient 1 which showed significant differences between words and pseudowords. In almost every case, activation of pseudowords meets or exceeds the degree of activation for words throughout the trial duration. The only exception to this qualitative pattern is channel 117, which shows a stronger peak for words than pseudowords in the early part of the trial. However, when averaged across the whole trial length, activity in response to pseudowords in channel 117 still outweighed activity in response to words (adjusted $p < 0.0001$).

Activity in response to pairwise sets of words and pseudowords (that is, pairs comparing each pseudoword with the word it was based on) can be compared within electrodes to examine whether acoustic tuning is represented in preferential responses for certain types of sounds. While the data for these within-electrode comparisons are too limited to quantify statistically, broad trends can be seen through visual inspection of the data. Figures 4, 5, and 6 plot by-stimulus activation patterns in pairwise groups for channel 117, channel 179 (the electrode with the largest average difference between words and pseudowords), and channel 100 (the electrode with the smallest difference). These patterns, while not unequivocal in every comparison in each electrode, suggest a general trend for heightened pseudoword over word activity across the comparisons shown.

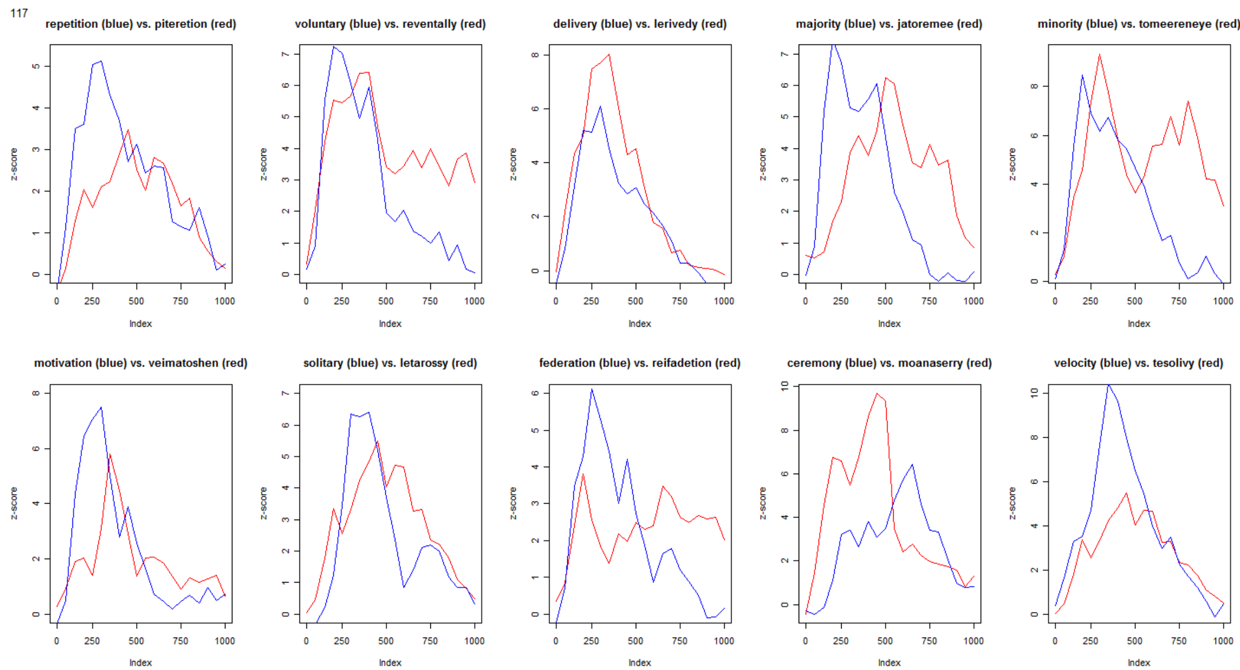

Figure 4: Activity for word-pseudoword pairs in electrode 117, patient 1

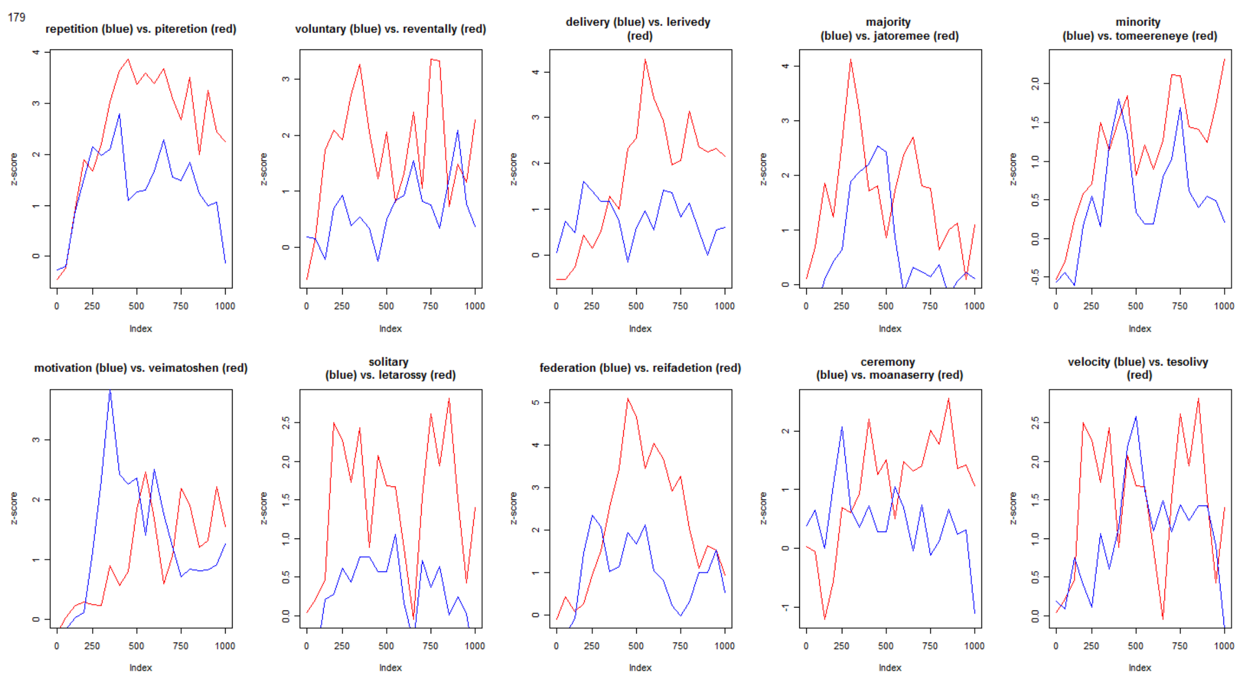

Figure 5: Activity for word-pseudoword pairs in electrode 179, patient 1

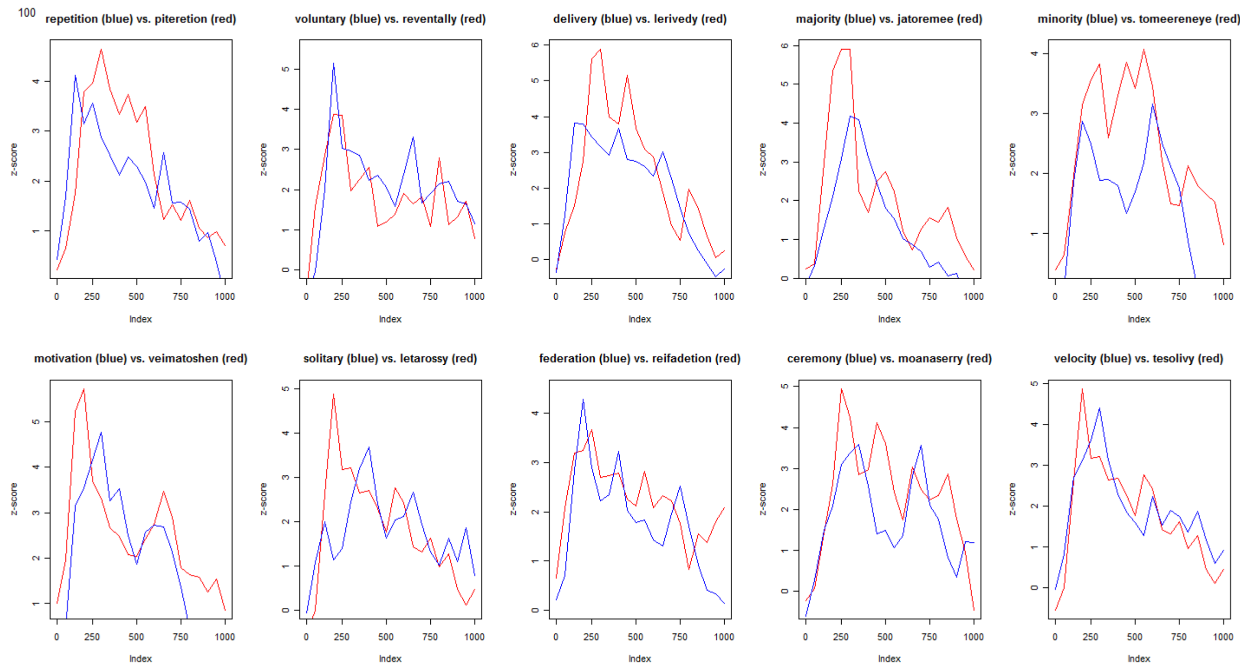

Figure 6: Activity for word-pseudoword pairs in electrode 100, patient 1

5 Discussion

This study aimed to explore the nature of early neural representations of words and pseudowords in auditory listening tasks. The current literature on lexical processing suggests three possibilities for the nature of word and pseudoword comprehension: (1) different pathways of activity, relying on sublexical information for pseudowords and lexical representations for words, (2) shared pathways through phonological processing, with higher-level lexical information accessed only by word stimuli, or (3) shared pathways with a lexical search for both words and pseudowords. The data presented here found no difference in the location of activity for words and pseudowords in the superior and middle temporal gyri, suggesting that early stages of listening and comprehension rely on the same processing pathways for words and pseudowords, rather than separate lexical and sublexical streams.

Critically, there were no electrodes in any patient which responded selectively to words but not pseudowords, which suggests that the processing pathways throughout listening and comprehension in this task were shared between the two stimuli types. However, it is difficult to fully distinguish between the second and third possibilities outlined above with the current data set, in part because the nature of listening during a listen-and-repeat task does not necessarily need to rely on higher-level lexical/semantic information in order for a proper behavioral response during repetition - it is possible to rely primarily on phonological representations. While it is likely that some semantic processing of words takes place automatically, there was not strong evidence in the middle temporal gyrus to conclusively determine that strong semantic activation was taking place.

However, indirect evidence for a degree of lexical processing comes from two sources. The first is the long latency of peak activation in pseudowords as opposed to words, which may be indicative of a prolonged search for the stimuli in the mental lexicon, and the first step to interface to a (failed) lexical search for these novel forms. The temporal unfolding of word/pseudoword differences supports this hypothesis, with a rapid decay after peak activation for words, but a sustained heightened activity for pseudowords, often through and past the end of the stimulus presentation.

The second piece of evidence is the pattern of lexical contrasts found in the superior temporal gyrus in patient 1. In this patient, posterior temporal lobe responses were insensitive to trial type, while more mid- and anterior temporal lobe electrodes showed increased sensitivity to trial type. This may be indicative of lexical processing along the ventral stream, as proposed in models by Hickok and Poeppel (2004, 2007) and Scott and Wise (2004). While the pathway of the ventral stream is usually localized to the MTG and inferior temporal lobe in these models, Gow et al. (2009) used Granger causality analysis to suggest phonological-to-semantic interfacing in both the MTG and some anterior STG sites, the latter of which is broadly consistent with the data from patient 1. There is less evidence for a ventral stream flow from pSTG to aSTG/MTG in the other patients, although the concentrating of lexically-sensitive electrodes the aSTG over the pSTG in patient 2 is not inconsistent with such an account; patient 3, by contrast, showed broad lexical specificity over the STG and cannot speak to this functional organization. Patients 2 and 3 did show a concentration of MTG activity in the posterior region near the superior temporal sulcus, which may be representative of an interface to the phonological network in the dorsal stream, as proposed by these models. Data from more patients would be informative in confirming and clarifying these patterns more broadly.

5.1 Acoustic tuning

In a more fine-grained analysis, patterns of activation from one patient were explored in order to test whether different responses to words and pseudowords shown in this data set reflect lexical properties or simply acoustic tuning to different classes of segments. Across these sets, pseudoword activation appears to be stronger in most comparisons, and for those where the opposite is true, there is no apparent segment-level pattern that would argue in favor of the hypothesis that differences are attributable solely to acoustic tuning. This suggests that the effects shown in this paper are not soley a function of the stimuli's acoustic properties. If they were, we might expect at least some comparisons to show strongly heightened activation for words at some time points and in some electrodes, reflecting a preference in those channels for the acoustics of segments more prominent in words. While it is very likely that acoustic tuning is observable in this data set when activity is examined at a finer temporal resolution, there appear to be lexical effects at the scale examined in the present study. This is evident in an overall trend for greater pseudoword activation across electrodes and stimulus pairs, as well as sustained heightened activity during pseudoword trials. Future work would benefit from the inclusion of spectrotemporal representations of neural activity, such as are found in STRF and ERSP encoding models (e.g. Pasley et al. 2012, Flinker et al. 2011), to fully account for these patterns.

6 Conclusion

The findings from this study suggest that pseudowords and words share strongly related processing pathways during listening and comprehension in tasks which utilize auditory presentation paradigms. Preliminary evidence has suggested that pseudowords may share ventral as well as dorsal pathways of activation, but more research is needed to clarify the extent to which these patterns generalize across individuals. Future work assessing the contribution of specific acoustic information to neural activity, as well as examinations of other regions in the pathways of neural lexical processing, will further clarify the extent to which the patterns demonstrated in this study dissociate the processing of spectrotemporal acoustic information from linguistic representations of phonological, lexical, and semantic information.

7 References

Bitterman, Y., Mukamel, R., Malach, R., Fried, I., and Nelken, I. (2008). Ultra-fine frequency tuning revealed in single neurons of human auditory cortex. Nature, 451(7175), 197-201.

Canolty, R. T., Soltani, M., Dalal, S. S., Edwards, E., Dronkers, N. F., Nagarajan, S. S., Kirsch, H. E., Barbaro, N. M., and Knight, R. T. (2007). Spatiotemporal dynamics of word processing in the human brain. Frontiers in neuroscience, 1(1):185-196.

Coltheart, M., Curtis, B., Atkins, P., and Haller, M. (1993). Models of reading aloud: Dual-route and parallel-distributed-processing approaches. Psychological Review, 100(4), 589-608.

Coltheart, M., Rastle, K., Perry, C., Langdon, R., and Ziegler, J. (2001). DRC: A dual route cascaded model of visual word recognition and reading aloud. Psychologial Review, 108(1), 204-256.

Crone, N. E., Boatman, D., Gordon, B., and Hao, L. (2001). Induced electrocorticographic gamma activity during auditory perception. Clinical Neurophysiology, 112(4):565-582.

Deacon, S. H. and Kirby, J. R. (2004). Morphological awareness: Just "more phonological"? The roles of morphological and phonological awareness in reading development. Applied Psycholinguistics, 25(02):223-238.

Edwards, E., Soltani, N., Deouell, L.Y., Berger, M.S., and Knight, R.T. (2005). High gamma activity in response to deviant auditory stimuli recorded directly from human cortex. *Journal of Neurophysiology* 94 (6), 42694280.

Flinker, A., Chang, E. F., Barbaro, N. M., Berger, M. S., and Knight, R. T. (2011). Sub-centimeter language organization in the human temporal lobe. Brain and Language, 117(3):103-109.

Glosser, G., Friedman, R. B., Kohn, S. E., Sands, L., and Grugane, P. (1998). Cognitive mechanisms for processing nonwords: Evidence from Alzheimers disease. Brain and Language, 63(1):32-49.

Hauk, O., Patterson, K., Woollams, A., Watling, L., Pulvermller, F., and Rogers, T. T. (2006). [q:] When would you prefer a SOSSAGE to a SAUSAGE? [a:] At about 100 msec. ERP correlates of orthographic typicality and lexicality in written word recognition. Journal of Cognitive Neuroscience, 18(5):818-832.

Hickok, G., and Poeppel, D. (2004). Dorsal and ventral streams: a framework for understanding aspects of the functional anatomy of language. Cognition, 92(1-2), 67-99.

Hickok, G. and Poeppel, D. (2007). The cortical organization of speech processing. Nature Reviews

Neuroscience, 8(5):393-402.

Mainy, N., Jung, J., Baciu, M., Kahane, P., Schoendorff, B., Minotti, L., Hoffmann, D., et al. (2008). Cortical dynamics of word recognition. Human brain mapping, 29(11), 1215-30. doi:10.1002/hbm.20457

Marshall, J. C., and Newcombe, F. (1973). Patterns of paralexia: A psycholinguistic approach. Journal of Psycholinguistic Research, 2(3):175-199.

Mechelli, A., Tempini, M. L. G., and Price, C. J. (2003). Neuroimaging studies of word and pseudoword reading: Consistencies, inconsistencies, and limitations. J. Cognitive Neuroscience, 15:260-271.

Newman, S. D. and Twieg, D. (2001). Differences in auditory processing of words and pseudowords: An fMRI study. Hum. Brain Mapp., 14(1):39-47.

Orfanidou, E., Marslen Wilson, W. D., and Davis, M. H. (2006). Neural response suppression predicts repetition priming of spoken words and pseudowords. J. Cognitive Neuroscience, 18:1237-1252.

Raettig, T. and Kotz, S. A. (2008). Auditory processing of different types of pseudo-words: An event-related fMRI study. NeuroImage, 39(3):1420-1428.

Scott, S., and Wise, R. (2004). The functional neuroanatomy of prelexical processing in speech perception. Cognition, 92(1-2), 13-45.

Seidenberg, M. S. and Mcclelland, J. L. (1989). A distributed developmental model of word recognition and naming. Psychological Review, 96:523-568.

Tanji, K., Suzuki, K., Delorme, A., Shamoto, H., and Nakasato, N. (2005). High-Frequency - Band activity in the basal temporal cortex during Picture-Naming and Lexical-Decision tasks. The Journal of Neuroscience, 25(13):3287-3293.

Tavabi, K., Elling, L., Dobel, C., Pantev, C., and Zwitserlood, P. (2009). Effects of Place of Articulation Changes on Auditory Neural Activity: A Magnetoencephalography Study. PLoS ONE, 4(2).

Towle, V. L., Yoon, H.-A., Castelle, M., Edgar, J. C., Biassou, N. M., Frim, D. M., Spire, J.-P., and Kohrman, M. H. (2008). ECoG gamma activity during a language task: differentiating expressive and receptive speech areas. Brain, 131(8):2013-2027.

Xiao, Z., Zhang, J. X., Wang, X., Wu, R., Hu, X., Weng, X., and Tan, L. H. (2005). Differential activity in left inferior frontal gyrus for pseudowords and real words: An event-related fMRI study on auditory lexical decision. Hum. Brain Mapp., 25(2):212-221.

A Appendix A: Stimuli

Words	Pseudowords
majority	jatoremee
delivery	lerivedy
solitary	letarossy
repetition	piteretion
federation	reifadetion
voluntary	reventally
velocity	tesolivy
minority	tomeereneye
motivation	veimatoshen

B Appendix B: Grid placement map

Figure 7: Location and arrangement of electrode grid in the left hemisphere, patient 1

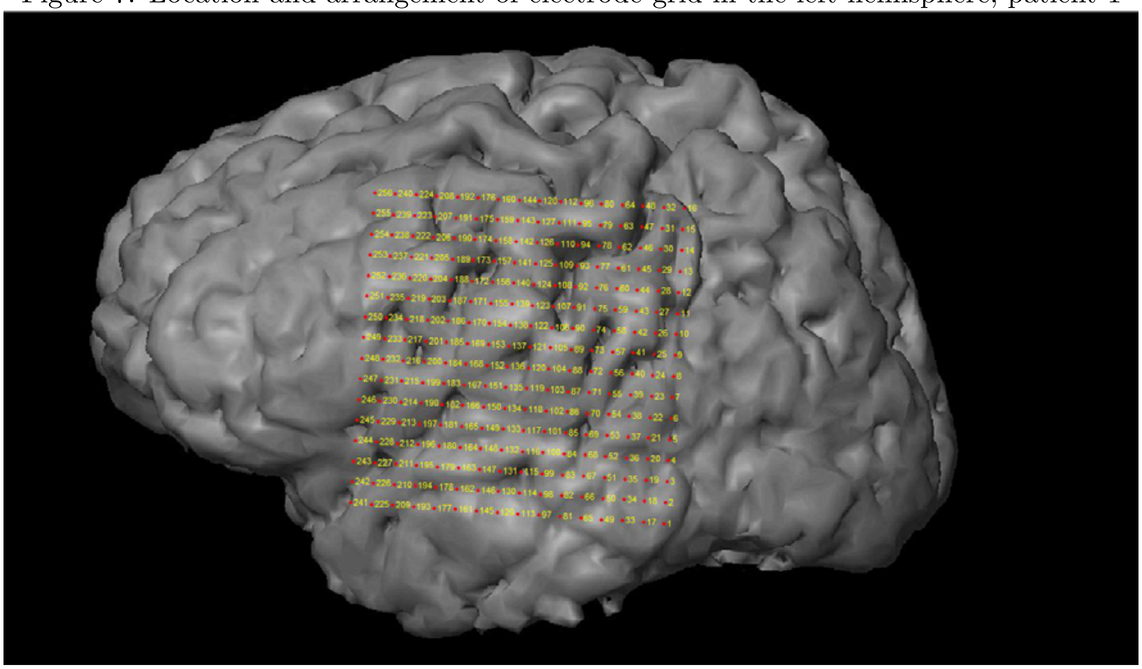

Figure 8: Location and arrangement of electrode grid in the left hemisphere, patient 2

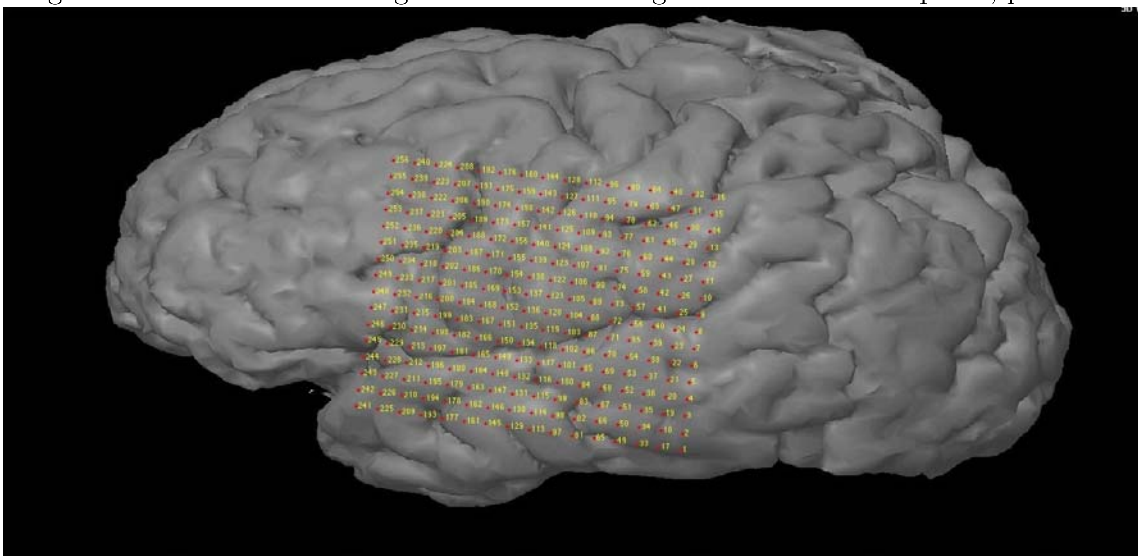

Figure 9: Location and arrangement of electrode grid in the left hemisphere, patient 3