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**Published on:** 23 May 2021 - [bioRxiv](#) (Cold Spring Harbor Laboratory)

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# A Spatiotemporal Map of Reading Aloud

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## 1 Abstract

2 Reading words aloud is a foundational aspect of the acquisition of literacy. The rapid rate at which  
3 multiple distributed neural substrates are engaged in this process can only be probed via  
4 techniques with high spatiotemporal resolution. We used direct intracranial recordings in a large  
5 cohort to create a holistic yet fine-grained map of word processing, enabling us to derive the  
6 spatiotemporal neural codes of multiple word attributes critical to reading: lexicality, word frequency  
7 and orthographic neighborhood. We found that lexicality is encoded by early activity in mid-fusiform  
8 (mFus) cortex and precentral sulcus. Word frequency is also first represented in mFus followed by  
9 later engagement of the inferior frontal gyrus (IFG) and inferior parietal sulcus (IPS), and  
10 orthographic neighborhood is encoded solely in the IPS. A lexicality decoder revealed high  
11 weightings for electrodes in the mFus, IPS, anterior IFG and the pre-central sulcus. These results  
12 elaborate the neural codes underpinning extant dual-route models of reading, with parallel  
13 processing via the lexical route, progressing from mFus to IFG, and the sub-lexical route,  
14 progressing from IPS to anterior IFG.

## 15 Introduction

16 Reading a word aloud requires multiple complex transformations in the brain - mapping the visual  
17 input of a letter string into an internal sequence of sound representations that are then expressed  
18 through orofacial motor articulations. Models of how this mapping occurs during reading invoke a  
19 dual-route architecture (Coltheart et al., 2001; Perry et al., 2007, 2010, 2019; Taylor et al., 2013),  
20 with a lexico-semantic route for rapidly reading known words and a sub-lexical route for constructing  
21 the phonology of novel words. A common method of targeting these two routes is to look at  
22 contrasts between phonological exception words and pseudowords (Fiebach et al., 2002; Sebastian  
23 et al., 2014; Shim et al., 2012; Taylor et al., 2013). Exception words contain irregular grapheme-  
24 phoneme associations (e.g. yacht, sew) and their phonologies must be retrieved from internal  
25 lexical representations as they cannot be accurately constructed *de novo*. In contrast, pseudowords  
26 have no stored representation and their phonology must be constructed rather than retrieved.

27 Ventral temporal cortex, particularly mid-fusiform cortex (mFus), is strongly associated with the  
28 lexical route. mFus is heavily implicated as the site of the orthographic lexicon, the long-term  
29 memory storage of which letter strings map onto known words (Glezer et al., 2015; Hirshorn et al.,  
30 2016; Kronbichler et al., 2004; Lochy et al., 2018; White et al., 2019; Woolnough et al., 2021). This  
31 region is sensitive to lexicality and word frequency (Kronbichler et al., 2004; White et al., 2019;  
32 Woolnough et al., 2021), and shows selective changes during visual word learning (Glezer et al.,  
33 2015; Taylor et al., 2019). The sub-lexical route, essential for articulating novel words, is thought to  
34 engage the inferior parietal lobe (IPL), dysfunction of which is associated with dyslexia (Raschle et  
35 al., 2011; Temple et al., 2003; Tomasino et al., 2020), dysgraphia (Rapp et al., 2016), in addition to  
36 phonological and semantic deficits (Binder et al., 2009; Hula et al., 2020; Numssen et al., 2021).  
37 The two routes are proposed to converge in the inferior frontal gyrus (IFG) (Taylor et al., 2013).

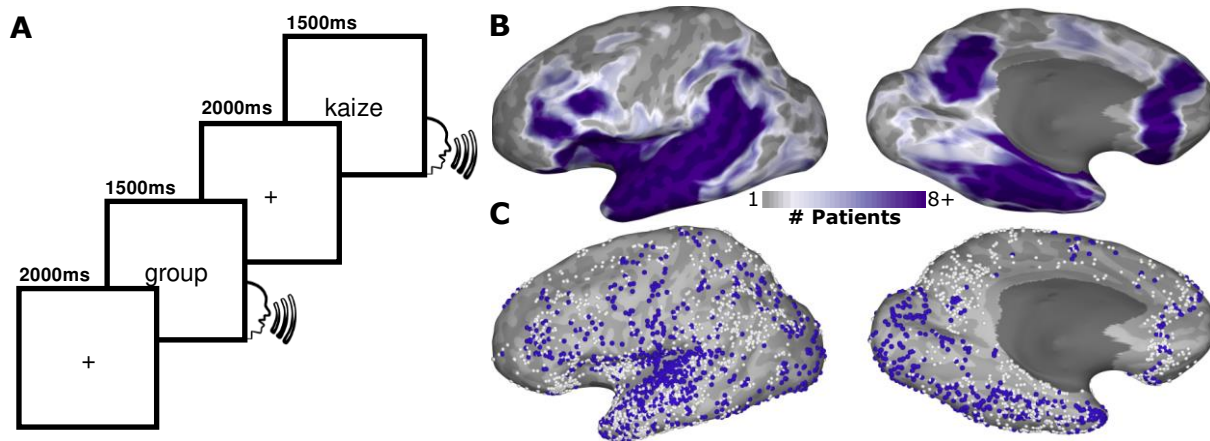
38 The majority of our knowledge regarding the neural architecture underlying reading aloud is derived  
39 from lesion data and functional MRI which provide accurate spatial localizations of function but lack  
40 crucial temporal information. We utilized intracranial recordings in a large cohort of patients (44  
41 patients, 3,642 electrodes), with medically intractable epilepsy, while they read aloud known and  
42 novel words. This allowed us to comprehensively map the flow of information through these cortical  
43 networks and track the spatiotemporal dynamics of the cortical representation of behaviorally  
44 relevant lexical and sub-lexical factors.

45

## 46 Results

47 Participants were visually presented with phonologically regular words, exception words and novel  
48 pseudowords that they read aloud (Figure 1A). Electrophysiological recordings were performed from  
49 a total of 3,642 separate intracranial electrodes placed for the localization of intractable epilepsy

50 (Figure 1B,C) - 4 participants had subdural grid electrodes (SDEs) and 40 had depth recordings  
51 using stereotactic EEG electrodes (sEEGs).



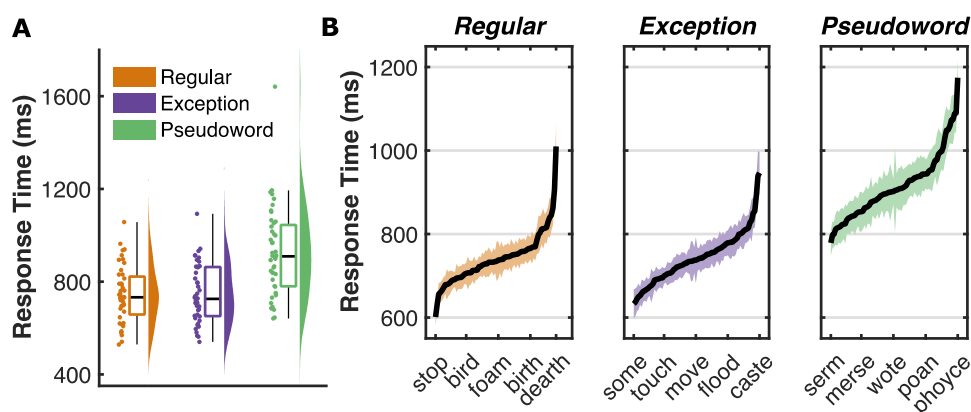
52

53 Figure 1: **Experimental Design and Electrode Coverage.** (A) Schematic representation of the  
54 reading task. (B) Representative coverage map (44 patients) and (C) individual electrode locations  
55 (3,642 electrodes) for the left hemisphere, highlighting responsive electrodes (1,158 electrodes;  
56 >20% activation above baseline).

57

## 58 Behavioral Analysis

59 Mean ( $\pm$  SD) response times (RTs) were: regular words ( $743 \pm 122$  ms), exception words ( $747 \pm$   
60  $125$  ms) and pseudowords ( $923 \pm 193$  ms) (Figure 2A). Regular and exception words showed no  
61 difference in RT (Wilcoxon sign rank,  $p = 0.75$ ;  $\ln(\text{Bayes Factor } (BF_{10})) = -1.5$ ) though pseudoword  
62 RT was slower than for exception words ( $p < 10^{-8}$ ,  $\ln(BF_{10}) = 28$ ).



63

64 Figure 2: **Population Word Response Times.** (A) Response time distribution for each of the three  
65 word classes, averaged within participant, (B) Mean ( $\pm$  SE) response times for each item within the  
66 three word classes, averaged across participants.

67

68 To determine the underlying properties of the words that modulate RT within this cohort, we  
69 performed linear mixed effects (LME) and Bayes factor (BF) analyses on each word class with fixed

70 effects modelling linguistic factors commonly linked to word identification and articulation (Table 1).  
 71 Regular words and exception word RTs showed the greatest modulation by word frequency.  
 72 Pseudoword RT was most strongly associated with orthographic neighborhood.

	Regular df = 3170, $r^2 = 0.36$			Exception df = 3098, $r^2 = 0.35$			Pseudowords df = 3185, $r^2 = 0.40$		
	$\beta$ (SE)	p	$\ln(\text{BF}_{10})$	$\beta$ (SE)	p	$\ln(\text{BF}_{10})$	$\beta$ (SE)	p	$\ln(\text{BF}_{10})$
<b>Length</b>	49 (17)	0.004	0.9	48 (22)	0.03	-0.7	23 (26)	0.38	-3
<b>Word Frequency</b>	-186 (17)	$<10^{-27}$	59	-154 (16)	$<10^{-21}$	43	-	-	-
<b>Orthographic Neighborhood</b>	52 (27)	0.05	-0.9	-97 (35)	0.005	1.4	227 (33)	$<10^{-11}$	21
<b>Phonological Neighborhood</b>	20 (18)	0.26	-2.5	-7 (16)	0.63	-3.2	58 (20)	0.004	0.5
<b>Positional Letter Frequency</b>	13 (14)	0.89	-2.9	-16 (16)	0.29	-2.9	-50 (19)	0.009	-0.3

73

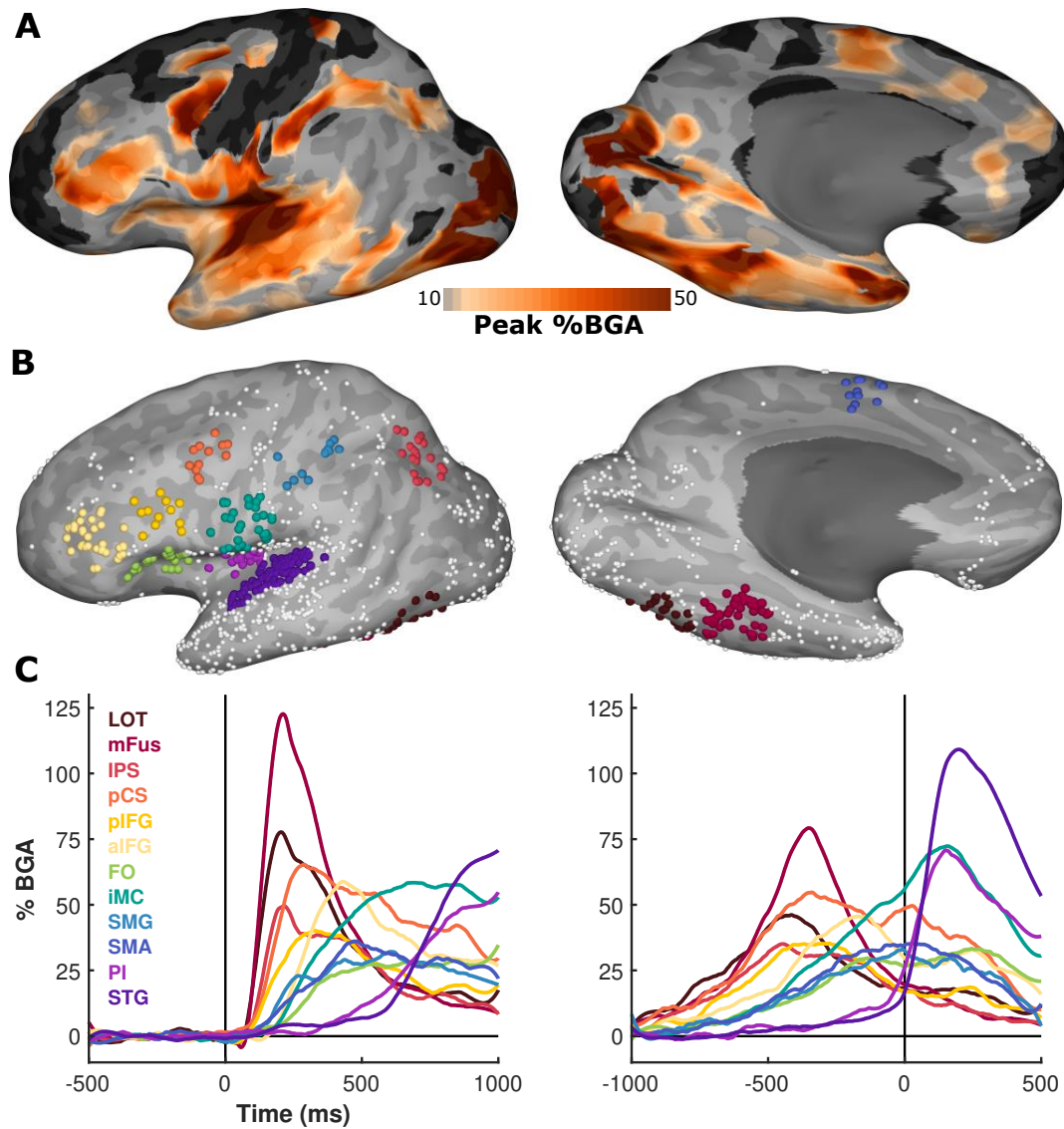
74 Table 1: **Statistical Modelling of Response Time**. As predictors were normalized,  $\beta$  values  
 75 approximate change in RT between extreme values within the entire stimulus set (Supplementary  
 76 Table 1). Factors with strong evidence of an effect ( $\ln(\text{BF}_{10}) > 2.3$ ) are highlighted.

77

## 78 Spatiotemporal Mapping of Single Word Reading

79 We used a mixed-effects, multilevel analysis (MEMA) of broadband gamma activity (BGA; 70-150  
 80 Hz) in group surface normalized space to create a population level map of cortical activation across  
 81 the population. This analysis is specifically designed to account for sampling variations and to  
 82 minimize effects of outliers (Argall et al., 2006; Conner et al., 2014; Esposito et al., 2013; Fischl et  
 83 al., 1999; Kadipasaoglu et al., 2014; Saad and Reynolds, 2012). All correctly articulated trials  
 84 across all word classes, were used. 4D representations of the spread of activation across the  
 85 cortical surface were generated by performing MEMA on short, overlapping time windows (150 ms  
 86 width, 10 ms spacing) to generate successive images of cortical activity, time locked to stimulus  
 87 onset (Video 1) or the onset of articulation (Video 2). The spatial distribution of activations was  
 88 highly comparable across word classes (Supplementary Figure 1).

89 By collapsing across these frames, we visualized peak activations at each point on the cortical  
 90 surface (Figure 3A). To create a more focused visualization of the spatiotemporal progression  
 91 across reading-sensitive cortex, we selected 12 regions of interest (ROIs) in areas thought to be  
 92 important to written word processing, speech production and speech monitoring (Figure 3B,C). This  
 93 analysis highlights regions displaying primarily pre-articulatory processes, in ventral  
 94 occipitotemporal cortex, inferior parietal lobe and the inferior frontal gyrus.



95

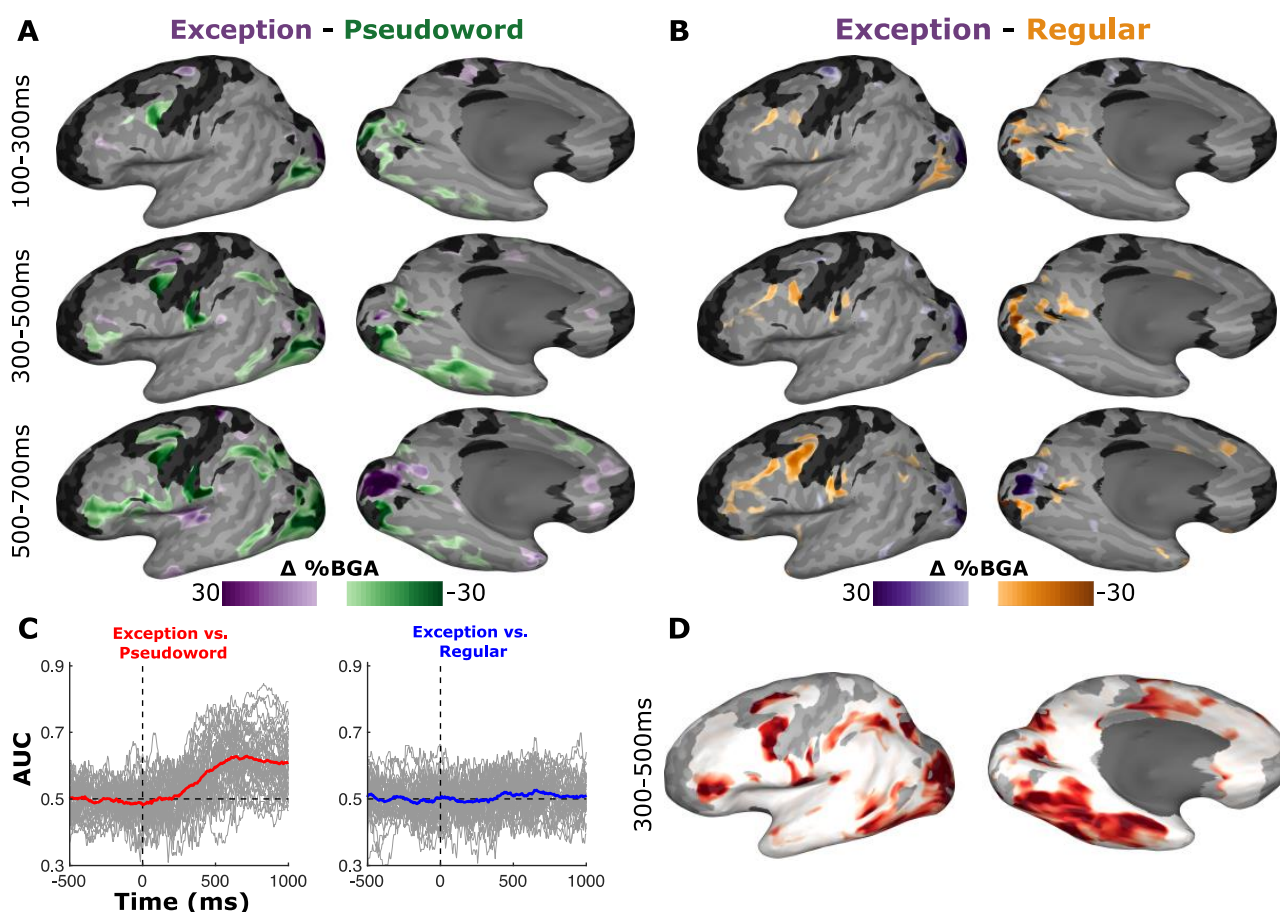
96 **Figure 3: Spatiotemporal Profile of Cortical Activations.** (A) Collapsed articulation-locked  
97 activation movie (Video 2) highlighting the amplitude of peak activation. (B) Representative ROIs in  
98 12 anatomically and functionally distinct regions, showing all responsive electrodes. (C) Mean  
99 activation during word reading of each ROI, averaged within patient, time locked to stimulus onset  
100 (left) and articulation onset (right). Standard errors omitted for visual clarity. LOT, Lateral  
101 OccipitoTemporal cortex; mFus, mid-Fusiform Cortex; IPS, Inferior Parietal Sulcus; pCS, pre-  
102 Central Sulcus; pIFG, posterior Inferior Frontal Gyrus; aIFG, anterior Inferior Frontal Gyrus; FO,  
103 Frontal Operculum; iMC, inferior Motor Cortex; SMG, Supra Marginal Gyrus; SMA, Supplementary  
104 Motor Area; PI, Posterior Insula; STG, Superior Temporal Gyrus.

105

### 106 **Spatiotemporal Representation of Lexical Factors**

107 To distinguish activity patterns across word classes we contrasted grouped gamma power  
108 activations between exception vs. pseudowords (lexicality) and exception vs. regular words  
109 (regularity) using MEMA. The lexicality contrasts demonstrated clusters in mFus, precentral sulcus  
110 (pCS), inferior parietal sulcus (IPS) and anterior inferior frontal gyrus (aIFG).

111 To determine how distinguishable whole-network activity patterns are for each of these factors,  
112 within-individuals at a single trial level, we used a logistic regression decoder. Decoders trained to  
113 distinguish between exception word and pseudoword trials demonstrated high decoding accuracy,  
114 with some patients showing >80% decoding accuracy (Figure 4C). These lexicality decoders  
115 displayed high electrode weightings across the ventral temporal surface, IPS, pCS and aIFG (Figure  
116 4D). Decoders trained to distinguish exception and regular words did not show higher decoding  
117 accuracy than in the baseline period.



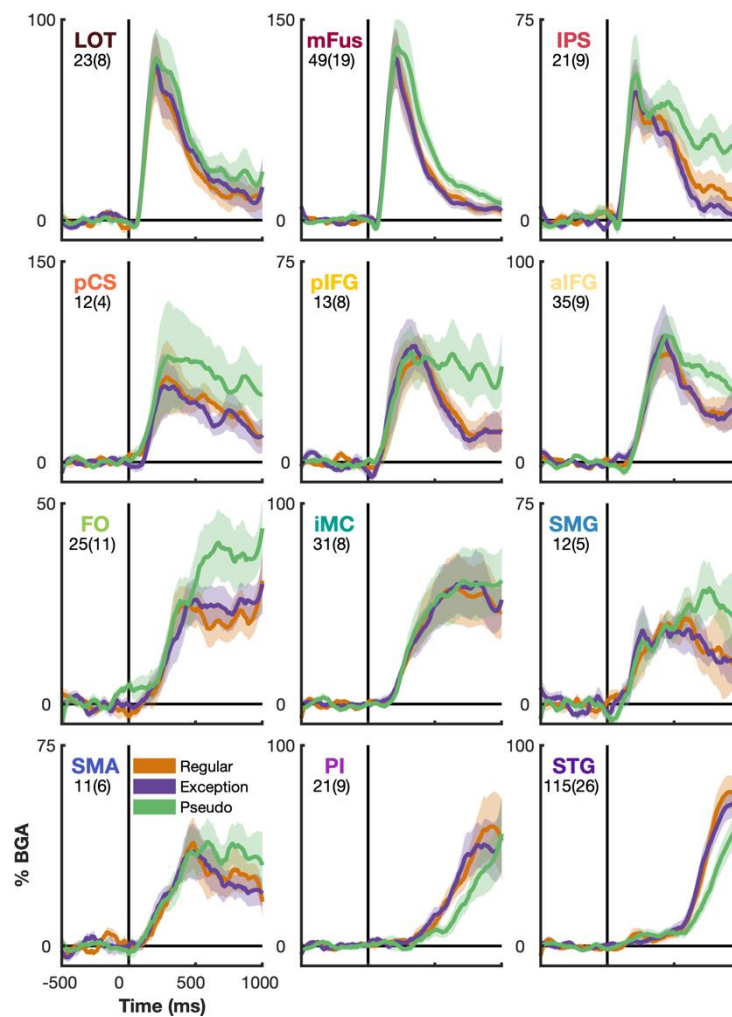
118

119 **Figure 4: Contrasting Word Classes.** (A,B) MEMA contrasts of (A) exception – pseudoword and  
120 (B) exception – regular, revealing regions of significantly different BGA between conditions ( $p < 0.01$   
121 corrected). Regions in black did not have consistent coverage for reliable MEMA results. (C)  
122 Decoding accuracies of the logistic regression decoders trained to distinguish exception word vs.  
123 pseudoword trials (left) and exception word vs regular word trials (right). Grey lines represent  
124 individual patient decoding accuracies. Colored line represents median accuracy. (D) Cortical  
125 surface representation of population average electrode weightings of the exception vs pseudoword  
126 decoder between 300 – 500 ms.

127

128 We observed lexicality distinctions between known words (regular and exception) and novel  
129 pseudowords broadly across the previously defined ROIs (Figure 5). These distinctions were  
130 observed earliest in mFus before spreading to pCS and visual word form regions, and subsequently

131 to IFG and IPS. Distinctions were also observed in post-articulatory auditory regions (posterior  
132 insula and superior temporal gyrus) relating to differences in RT between known and novel words.



133

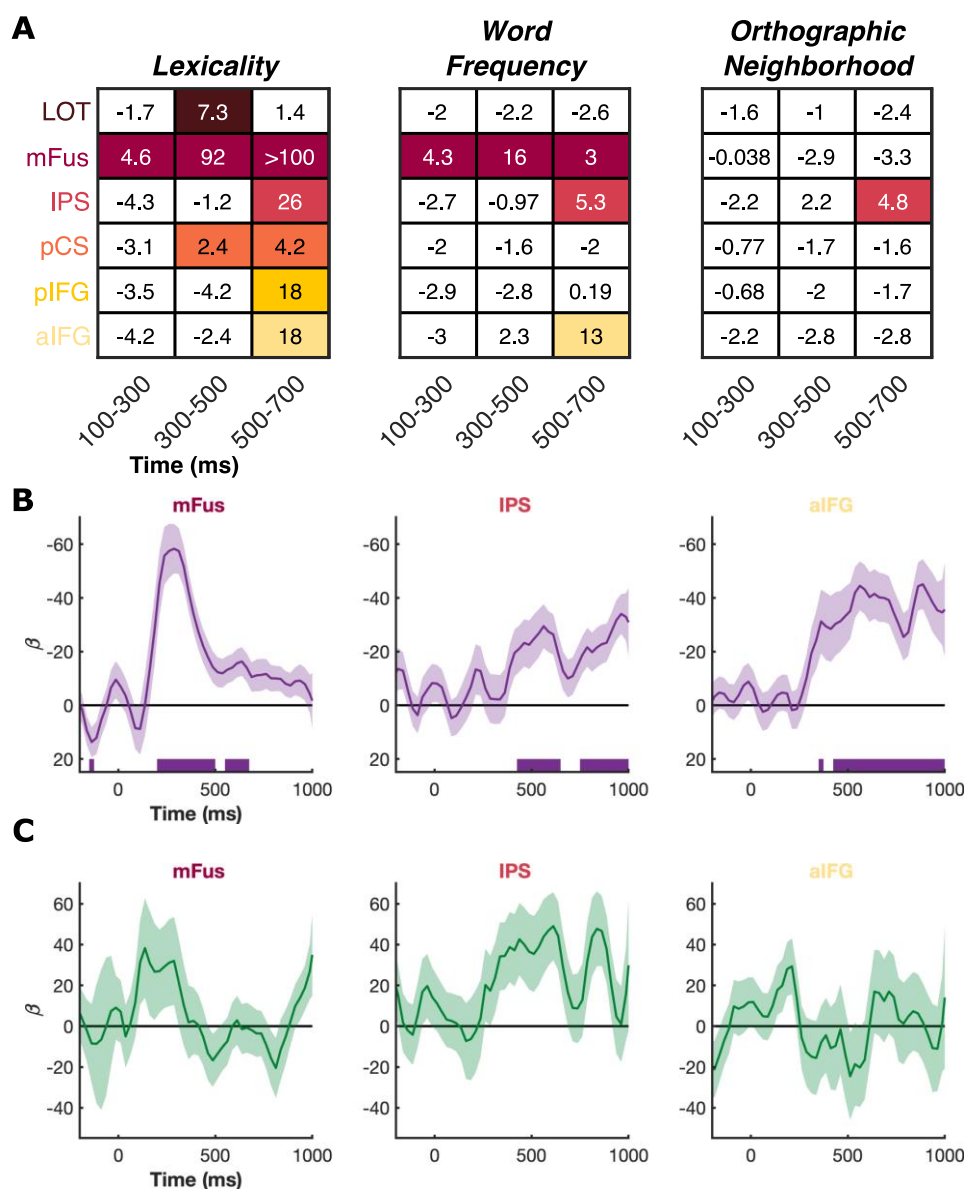
134 **Figure 5: Spatiotemporal Activation Profiles of Known and Novel Words.** Mean activation ( $\pm$   
135 SE) for each word class, within each ROI, during word reading, averaged within patient, time locked  
136 to stimulus onset. Number of electrodes and patients, per ROI, is indicated. LOT, Lateral  
137 OccipitoTemporal cortex; mFus, mid-Fusiform Cortex; IPS, Inferior Parietal Sulcus; pCS, pre-  
138 Central Sulcus; pIFG, posterior Inferior Frontal Gyrus; aIFG, anterior Inferior Frontal Gyrus; FO,  
139 Frontal Operculum; iMC, inferior Motor Cortex; SMG, Supra Marginal Gyrus; SMA, Supplementary  
140 Motor Area; PI, Posterior Insula; STG, Superior Temporal Gyrus.

141

142 For the six ROIs that showed a clear pre-articulatory peak in activation, we analyzed their activity for  
143 sensitivity to the main drivers of RT seen in the behavioral analysis; lexicality, word frequency of  
144 known words and orthographic neighborhood of pseudowords. mFus showed the earliest sensitivity  
145 to lexicality, followed by LOT and pCS, and then broad sensitivity across multiple regions (Figure  
146 6A). mFus showed an early and long-lasting word frequency sensitivity, with IPS and aIFG  
147 becoming sensitive later (500-700 ms). Sensitivity to orthographic neighborhood of pseudowords  
148 was only seen in IPS (500-700 ms).



149 For the three regions we found to have evidence of word frequency or orthographic neighborhood  
 150 sensitivity, mFus, IPS and aIFG, we used LME models at a higher time resolution. Sensitivity to  
 151 word frequency was observed earliest in mFus (200 ms) followed by IPS and aIFG (425 ms) (Figure  
 152 6B). In IPS we observed a period of elevated orthographic neighborhood sensitivity, but this did not  
 153 show significance at this time resolution (Figure 6C).



154

155 **Figure 6: Regression of Lexical Factors.** (A) Bayes factor analysis of lexicality, word frequency  
 156 and orthographic neighborhood effects in the six pre-articulatory ROIs, for three time windows.  
 157 Lexicality tested all known words against pseudowords. Word frequency was regressed across all  
 158 known words. Orthographic neighborhood was regressed across all pseudowords. Bayes factor  
 159 ( $\ln(BF_{10})$ ) shown for each contrast and values  $>2.3$  are highlighted. (B,C) Linear mixed effects  
 160 (LME) model regression of (B) word frequency in known words and (C) orthographic neighborhood  
 161 in pseudowords, in three ROIs ( $\beta \pm SE$ ; mFus, 49 electrodes, 19 patients; IPS, 21 electrodes, 9  
 162 patients; aIFG, 35 electrodes, 9 patients). Colored bars represent regions of significance ( $q < 0.05$ ).

163

## 164 **Discussion**

165 This large population intracranial study comprehensively maps the spatiotemporal spread of cortical  
166 activation across the left hemisphere during word reading to derive the dynamics of cortical  
167 networks underlying literacy. Dual-route architectures of reading networks (Coltheart et al., 2001;  
168 Perry et al., 2007, 2010, 2019), derived on behavioral and lesional data, imply separable processing  
169 routes for known vs novel words. We find a network of regions sensitive to lexicality, initially the  
170 mFus and pCS, then spreading broadly across IPS and IFG. The spatial distribution of this lexicality  
171 effect is broadly comparable with the lexicality network identified with fMRI (Heim et al., 2013; Taylor  
172 et al., 2013, 2014), with the added benefit of millisecond temporal resolution. Responses in lexicality  
173 sensitive regions maximally separate for known and novel words between 300-500ms after stimulus  
174 onset, in a manner that is reliable enough to enable single trial decoding of lexicality. These data  
175 minimize the impact of response time variations, which confounds modalities with lower temporal  
176 resolution (e.g. fMRI) and may artificially inflate lexicality effects in regions such as IFG (Taylor et  
177 al., 2014).

178 We have previously demonstrated that mFus is the earliest region in ventral temporal cortex to show  
179 sensitivity to word frequency while reading (Woolnough et al., 2021). It is commonly assumed that  
180 sensitivity to statistical properties of language such as word frequency seen in ventral temporal  
181 cortex are as a result of top-down modulation from IFG (Heim et al., 2013; Price and Devlin, 2011;  
182 Woodhead et al., 2014). Here, we demonstrate again the primacy of the mFus in coding both word  
183 frequency and lexicality, preceding the engagement of aIFG and IPS in these processes by over  
184 200 ms. This consolidates mFus's role as a specialized orthographic lexicon, organized based on  
185 statistical regularities of individual words in natural language.

186 The IPS was the only region with sensitivity to orthographic neighborhood. This sensitivity likely  
187 reflects grapheme-phoneme conversion processes in this region (Dehaene-Lambertz et al., 2018;  
188 Xu et al., 2020). Given that IPS shows both word frequency and lexicality sensitivity, its role in sub-  
189 lexical processing might appear to be questionable. However, for known words, the lexical route is  
190 faster and more accurate than the sub-lexical route – thus, once a letter string is identified as a  
191 known lexical object, sub-lexical processes are no longer required. Given the word frequency  
192 dependence of lexical identification, the timing of the cessation of sub-lexical processes should also  
193 be frequency dependent. This interpretation is entirely consistent with our data as IPS shows more  
194 sustained activity, but not higher peak activity for novel words.

195 It is theorized that pCS is involved in articulatory phonological processing, specifically feedforward  
196 control of articulator velocity (Matchin and Hickok, 2020; Tourville and Guenther, 2011). Through  
197 lesion studies pCS has also been linked to phonological dyslexia (Rapcsak et al., 2009; Tomasino  
198 et al., 2020). Our data demonstrate that pCS activation begins early, preceding the IFG, suggesting  
199 a role in early linguistic or phonological processing, potentially as part of the sub-lexical route. pCS  
200 demonstrates lexical sensitivity but no effect of word frequency. Given the association of pCS with

201 articulation phonology and phonological dyslexia, this may represent part of the process of  
202 constructing novel phonologies.

203 This study provides further evidence that medial frontal operculum is involved in pre-articulatory,  
204 preparatory processes, distinct from those of the lateral IFG (Mälfiia et al., 2018; Woolnough et al.,  
205 2019). Lesions involving this region have been linked to impairment of complex articulation (Baldo  
206 et al., 2011) which may explain the greater engagement during pseudoword articulation.

207 We observed no significant pre-articulatory activity in middle temporal gyrus or angular gyrus,  
208 regions that have been linked to semantic and phonological processes during word processing  
209 (Graves et al., 2010; Hartwigsen et al., 2010; Sliwiska et al., 2015; Stoeckel et al., 2009). These  
210 regions appear to be engaged during reading in children but may not be recruited in adults for  
211 simple reading tasks (Martin et al., 2015), instead being used primarily for comprehending multi-  
212 word phrases (Dronkers et al., 2004; Fridriksson et al., 2018; Matchin et al., 2017).

213

## 214 **Materials and Methods**

215 Participants: 44 patients (25 male, 19-60 years, 5 left-handed, IQ  $94 \pm 15$ , Age of Epilepsy Onset  $18$   
216  $\pm 9$  years) participated in the experiments after giving written informed consent. All participants were  
217 semi-chronically implanted with intracranial electrodes for seizure localization of pharmaco-resistant  
218 epilepsy. Participants were excluded if they had confirmed right-hemisphere language dominance or  
219 a significant additional neurological history (e.g. previous resections, MR imaging abnormalities  
220 such as malformations or hypoplasia). All experimental procedures were reviewed and approved by  
221 the Committee for the Protection of Human Subjects (CPHS) of the University of Texas Health  
222 Science Center at Houston as Protocol Number HSC-MS-06-0385.

223 Electrode Implantation and Data Recording: Data were acquired from either subdural grid  
224 electrodes (SDEs; 4 patients) or stereotactically placed depth electrodes (sEEGs; 40  
225 patients). SDEs were subdural platinum-iridium electrodes embedded in a silicone elastomer sheet  
226 (PMT Corporation; top-hat design; 3mm diameter cortical contact), and were surgically implanted  
227 via a craniotomy (Pieters et al., 2013; Tandon, 2012; Tong et al., 2020). sEEGs were implanted  
228 using a Robotic Surgical Assistant (ROSA; Medtech, Montpellier, France) (Rollo et al., 2020;  
229 Tandon et al., 2019). Each sEEG probe (PMT corporation, Chanhassen, Minnesota) was 0.8 mm in  
230 diameter and had 8-16 electrode contacts. Each contact was a platinum-iridium cylinder, 2.0 mm in  
231 length and separated from the adjacent contact by 1.5 - 2.43 mm. Each patient had 12-20 such  
232 probes implanted. Following surgical implantation, electrodes were localized by co-registration of  
233 pre-operative anatomical 3T MRI and post-operative CT scans in AFNI (Cox, 1996). Electrode  
234 positions were projected onto a cortical surface model generated in FreeSurfer (Dale et al., 1999),  
235 and displayed on the cortical surface model for visualization (Pieters et al., 2013). Intracranial data  
236 were collected during research experiments starting on the first day after electrode implantation for

237 sEEGs and two days after implantation for SDEs. Data were digitized at 2 kHz using the NeuroPort  
238 recording system (Blackrock Microsystems, Salt Lake City, Utah), imported into Matlab, initially  
239 referenced to the white matter channel used as a reference for the clinical acquisition system and  
240 visually inspected for line noise, artifacts and epileptic activity. Electrodes with excessive line noise  
241 or localized to sites of seizure onset were excluded. Each electrode was re-referenced to the  
242 common average of the remaining channels. Trials contaminated by inter-ictal epileptic spikes were  
243 discarded.

244 Stimuli and Experimental Design: All patients undertook a word reading task. Stimuli were  
245 presented on a 2,880 x 1,800 pixel, 15.4" LCD screen positioned at eye-level, 2-3' from the patient.  
246 Participants were presented with 80 each of monosyllabic (i) phonologically regular words, (ii)  
247 phonologically irregular exception words and (iii) novel pseudowords and asked to read them aloud.  
248 Stimuli were presented using Psychophysics Toolbox (Kleiner et al., 2007) in Matlab, in all lower-  
249 case letters, in Arial font with a height of 150 pixels (~2.2° visual angle). Each stimulus was  
250 displayed for 1,500 ms with an inter-stimulus interval of 2,000 ms. Stimuli were presented in two  
251 recording sessions, each containing presentation of 120 stimuli in a pseudorandom order with no  
252 repeats.  $95 \pm 4\%$  of trials were correctly articulated. The most common errors were regularization of  
253 exception words (e.g. sew as *sue*, soot as *sute*) or lexicalization of pseudowords (e.g. shret as  
254 *shirt*, jinje as *jingle*).

255 Signal Analysis: Analyses were performed by first bandpass filtering raw data of each electrode into  
256 broadband gamma activity (BGA; 70-150Hz) following removal of line noise (zero-phase 2nd order  
257 Butterworth bandstop filters). A frequency domain bandpass Hilbert transform (paired sigmoid flanks  
258 with half-width 1.5 Hz) was applied and the analytic amplitude was smoothed (Savitzky - Golay finite  
259 impulse response, 3rd order, frame length of 201 ms). BGA is presented here as percentage  
260 change from baseline level, defined as the period -500 to -100 ms before each word presentation.

261 Electrodes were tested to see if they were responsive during the task. Responsiveness was defined  
262 as displaying >20% average BGA over baseline for at least one of the three following windows: 100  
263 to 500 ms following stimulus onset, -500 to -100 ms before articulation onset or 100 to 500 ms  
264 following articulation onset. Of the 3,642 useable electrodes, 1,158 electrodes were designated  
265 responsive based on these criteria.

266 Neural Decoding: Decoding analyses were performed using logistic regression classifiers, using 5-  
267 fold cross validation, implemented within MNE-Python (Gramfort, 2013; Gramfort et al., 2014). For  
268 each patient, decoding performance was summarized with an area under the curve (AUC) and a set  
269 of classifier weights for each electrode. Temporal decoding was performed on BGA using a sliding  
270 estimator at each time point, using all available electrodes. Spatial distribution of classifier weights  
271 was reconstructed by a cortical surface transform onto a standardized brain surface using each  
272 electrode's presumed "recording zone", an exponentially decaying geodesic radius (Kadipasaoglu et

273 al., 2014). Cortical surface maps were amplitude normalized within patient then averaged across  
274 patient to create a population weighting map.

275 Linguistic Analysis: We quantified word frequency as the base-10 log of the SUBTLEXus frequency  
276 (Brysbaert and New, 2009). This resulted in a frequency of 1 meaning 10 instances per million  
277 words and 4 meaning 10,000 instances per million words. There was no significant difference  
278 between word frequency of regular ( $1.5 \pm 0.35$ ; Mean  $\pm$  SD) and exception ( $1.7 \pm 1.0$ ) words  
279 (Wilcoxon rank sum,  $p = 0.36$ ). Positional letter frequency was calculated as the base-10 log of the  
280 sum of the SUBTLEXus frequencies of all words with a given letter in a specific ordinal position.  
281 Orthographic neighborhood was quantified as the orthographic Levenshtein distance (OLD20); the  
282 mean number of single character edits required to convert the word into its 20 nearest neighbors  
283 with a log frequency greater than 0 (Yarkoni et al., 2008). Phonological neighborhood densities  
284 were obtained from the Irvine Phonotactic Online Dictionary (IPhOD) (Vaden et al., 2009).  
285 Pseudowords were phonemically transcribed using the most common pronunciation.

286 **Acknowledgements**

287 We express our gratitude to all the patients who participated in this study; the neurologists at the  
288 Texas Comprehensive Epilepsy Program who participated in the care of these patients; and the  
289 nurses and technicians in the Epilepsy Monitoring Unit at Memorial Hermann Hospital who helped  
290 make this research possible. This work was supported by the National Institute of Neurological  
291 Disorders and Stroke NS098981.

292 **Author Contributions**

293 Conceptualization: OW, CD, SD, NT; Methodology: OW, CD, NT; Data curation: OW, CD, PSR, ZR;  
294 Software: OW, CD, AC; Formal Analysis: OW, AC; Writing – Original Draft: OW; Writing – Review  
295 and Editing: OW, SD, SFB, NT; Visualization: OW; Funding Acquisition: NT; Neurosurgical  
296 Procedures: NT.

297 **Declaration of Interests**

298 The authors declare no competing interests

299

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- 444

445 **Supplementary Information**

446 Video 1: **Spread of Stimulus-Locked Activity across the Cortical Surface.** MEMA movie of the  
 447 time course of broadband gamma activation across the cortical surface with trials time-locked to  
 448 onset of the visual stimulus. Regions in black did not have consistent coverage for reliable MEMA  
 449 results.

450

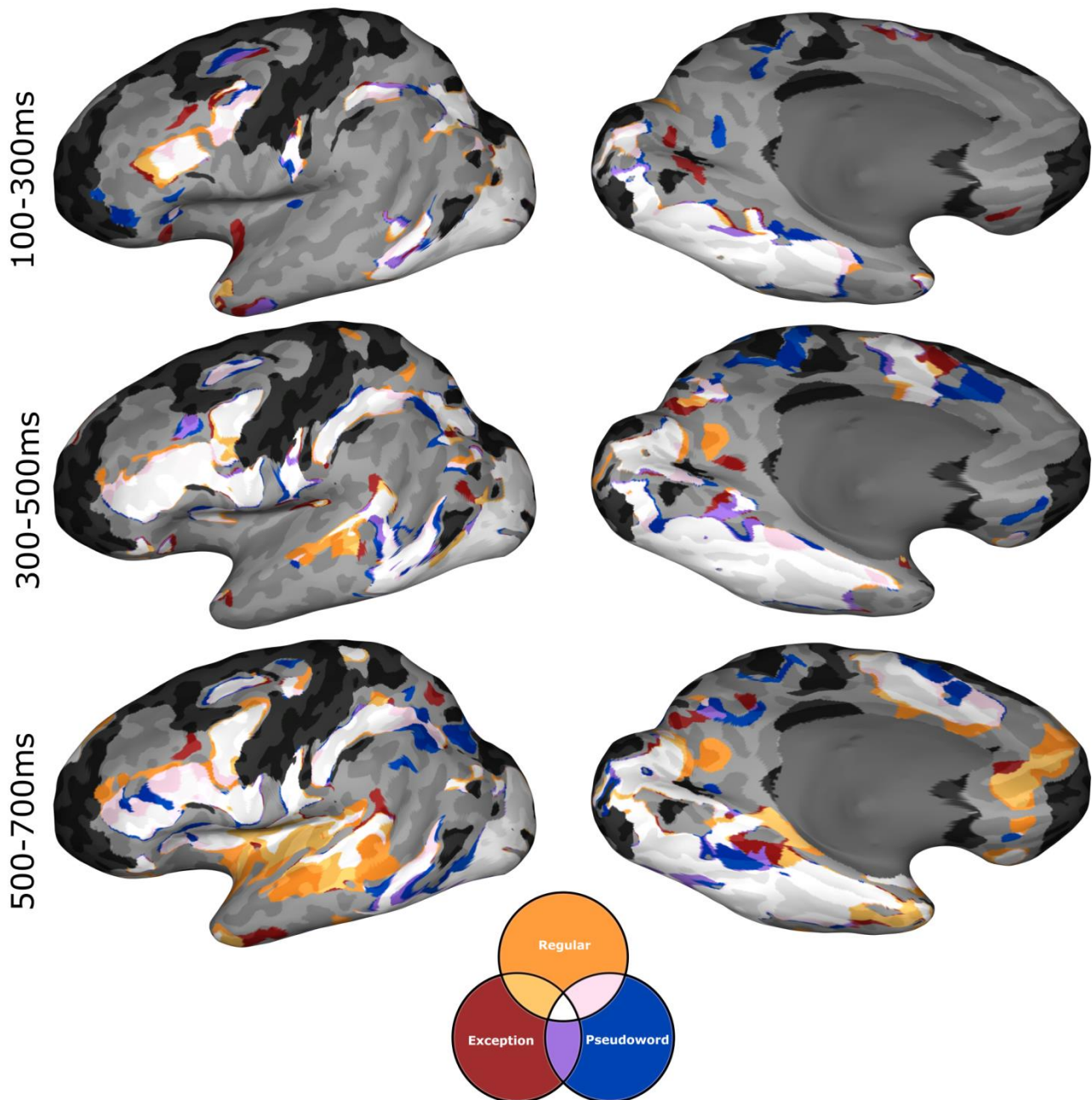
451 Video 2: **Spread of Articulation-Locked Activity across the Cortical Surface.** MEMA movie of  
 452 the time course of broadband gamma activation across the cortical surface with trials time locked to  
 453 the onset of articulation. Regions in black did not have consistent coverage for reliable MEMA  
 454 results.

455

	All			Regular			Exception			Pseudowords		
	Min	Med	Max	Min	Med	Max	Min	Med	Max	Min	Med	Max
<b>Length</b>	3	4	6	3	4	6	3	4	6	4	4	6
<b>Word Frequency</b>	-1	1.7	3.8	-1	1.7	3	-0.5	1.8	3.8	-	-	-
<b>Orthographic Neighborhood</b>	1	1.7	2.8	1	1.8	2.4	1	1.6	2	1.2	1.9	2.8
<b>Phonological Neighborhood</b>	0	22	49	6	24	42	1	22	49	0	19	41
<b>Positional Letter Frequency</b>	4.4	4.9	5.2	4.4	4.9	5.1	4.5	4.9	5.1	4.5	4.8	5.2

456 Supplementary Table 1: **Distribution of Statistical Regressors.** Minimum, median and maximum  
 457 values for each of the regressors used, across the whole stimulus set and for individual word  
 458 classes. Statistical models used normalized data, subtracting the minimum value and dividing by the  
 459 range across the whole stimulus set.

460



461

462 Supplementary Figure 1: **Conjunction Map of Word Class Activations.** MEMA conjunction maps  
463 showing overlap of binarized activation maps of each of the three word classes tested ( $\%BGA >$   
464  $5\%$ ,  $t > 2.58$ , patients  $\geq 3$ ), over three time windows locked to stimulus onset. Across all time  
465 windows all three word classes demonstrate a gross overlap of activation (white). In the later time  
466 window, areas associated with post-articulatory processes (e.g. auditory cortex) show selective  
467 activation for known words, reflecting differences in response time between known words and novel  
468 pseudowords. Regions in black did not have consistent coverage for reliable MEMA results.