

Thalamic encoding of lexical status is lateralized during reading aloud

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Abstract

To explore whether the thalamus participates in lexical status encoding, local field potentials were recorded in patients undergoing deep brain stimulation lead implantation while they read aloud single-syllable words and nonwords. Bilateral decreases in thalamic beta (12-30Hz) activity were preferentially locked to stimulus presentation, and these decreases were greater when nonwords were read. Increased broadband gamma (70-150Hz) activity also was locked preferentially to speech onset bilaterally, but greater nonword-related increases in this activity were observed only on the left, demonstrating lateralization of thalamic gamma selectivity for lexical status. In addition, this lexical status effect was strongest in more anterior thalamic locations, regions which are more likely to receive pallidal than cerebellar afferents. These results provide evidence from intracranial thalamic recordings for the lateralization and topography of subcortical lexical status processing.

1 **Introduction**

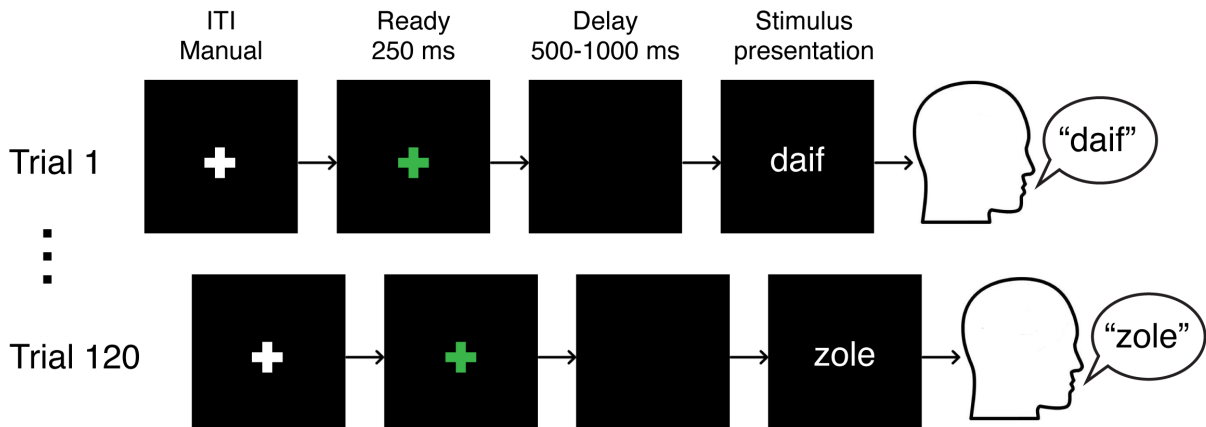
2 Reading words aloud depends on our ability to transform information about letter combinations
3 into plans for producing speech sounds. Determining whether a group of letters represents a
4 word is one important component of this process. While word reading can be supported by
5 processes that permit mapping entire word forms to lexical representations, nonword reading
6 depends upon sublexical processes that map spelling and sound (Coltheart et al., 2001).
7 Functional neuroimaging has allowed for increasingly detailed study of the cortical regions that
8 participate in these phonological processes, for instance demonstrating that a region of the
9 inferior frontal gyrus (Brodmann's areas 44 and 45) is significantly more active for nonword
10 reading than for word reading (Fiez et al., 1999; Hagoort et al., 1999; Heim et al., 2005;
11 Herbster et al., 1997). The role of subcortical regions in spoken word production remains
12 elusive, however, due to the low resolution of neuroimaging techniques for measuring
13 subcortical activity. Resolving this knowledge gap is important, given that cortical activity is
14 modulated by thalamic outflow through basal ganglia-thalamo-cortical and cerebello-thalamo-
15 cortical circuits (Behrens et al., 2003; Bosch-Bouju et al., 2013; Hwang et al., 2017; Zhang et
16 al., 2010). Despite the cortico-centric focus of most experimental work and accompanying
17 models, there is increasing recognition of the role of subcortical processes in language
18 production (Llano, 2015).

19
20 Neurosurgical procedures involving invasive recording and stimulation in epilepsy patients
21 undergoing electrode implantation for seizure mapping traditionally have provided the only direct
22 means to test hypotheses related to cortical function during reading (Juphard et al., 2011).
23 Epilepsy surgery, however, rarely provides access to the thalamus and basal ganglia.
24 Movement disorders surgery, on the other hand, routinely provides direct access to the
25 thalamus and basal ganglia in awake patients. Regionalization of language function within the
26 left thalamus was established in surgery for movement disorders in the 1970s, in seminal
27 studies by Ojemann and colleagues that employed electrical stimulation principles borrowed
28 from traditional cortical language mapping protocols (Johnson & Ojemann, 2000). More
29 recently, event-related potential recordings in patients undergoing deep brain stimulation (DBS)
30 have suggested that thalamic structures are engaged in the analysis of syntactic, semantic and
31 lexical information during acoustically presented language tasks (Tiedt et al., 2017; Wahl et al.,
32 2008).

33

34 We recently developed a protocol to study subcortical activity during single-syllable
35 word/nonword reading, in patients undergoing DBS lead implantation (Chrabaszcz et al., 2019;
36 Lipski et al., 2018). Here, we explore whether the thalamus participates in the encoding of
37 lexical status, by recording local field potentials (LFP) in patients undergoing DBS lead
38 implantation for essential tremor targeting the ventral intermediate nucleus of the thalamus
39 (Vim, which corresponds to the ventral portion of the ventral lateral posterior nucleus (VLp)
40 (Macchi & Jones, 1997)). Subjects performed a reading aloud task where they were asked to
41 read aloud single-syllable words or nonwords that appeared on a computer screen (Figure 1).
42 We assessed thalamic participation in lexical status encoding by comparing task-related neural
43 responses when participants spoke nonwords vs. words.

44



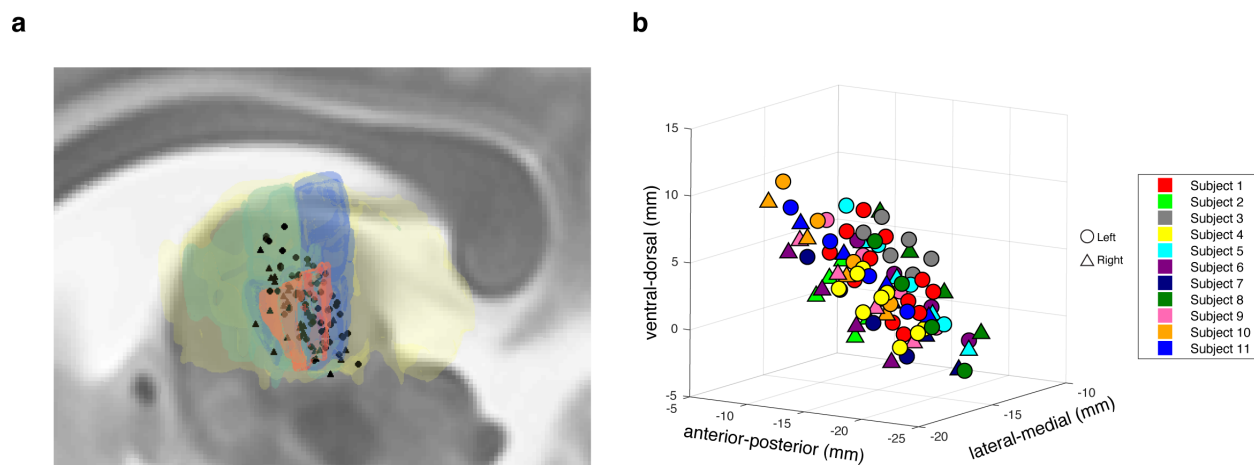
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46 **Figure 1: Schematic of experiment.** ITI: inter-trial interval.

47

48 Results

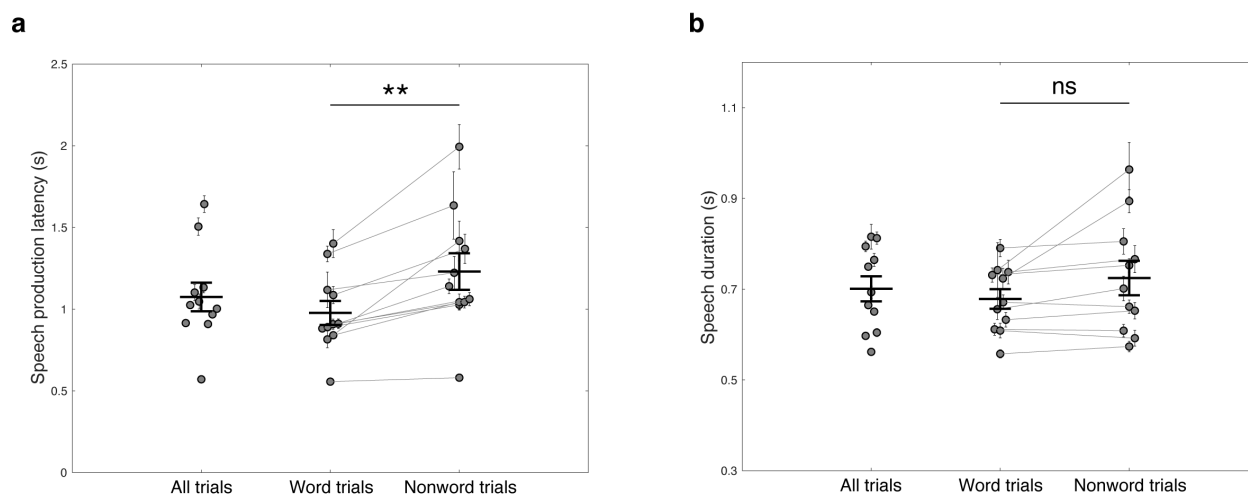
49 Eleven subjects read aloud single-syllable words alternating with nonwords, intraoperatively
50 during implantation of DBS leads targeting the Vim nucleus of the thalamus. LFP recordings in
51 four subjects were obtained unilaterally (3 left, 1 right) during microelectrode mapping, where
52 each of these subjects performed up to four sessions of 120 trials. Recordings from seven
53 subjects were obtained from DBS lead contacts, where each of these subjects performed two
54 sessions: in the first session unilateral recordings were made from the left thalamus, and in the
55 second session bilateral recordings were performed simultaneously. A total of 117 recordings
56 (data recorded in one location in one session) from 89 recording sites pooled across subjects
57 were collected. Recording locations were determined in MNI (Montreal Neurological Institute)
58 space (Figure 2) and comprised locations within or bordering (within 1mm) the ventral anterior
59 nucleus (VA) and the ventral lateral anterior nucleus (VL_a) (38/89), or the VL_p (51/89).



60
61 **Figure 2: Localization and MNI-transformation of recording sites.** **a** Sagittal view of the
62 recording locations of all the subjects relative to the thalamus (yellow), VA and VLa (green), VLp
63 (blue), and Vim (orange), superimposed on a T2-weighted image. **b** A plot of all the recording
64 sites in MNI space with their MNI-defined coordinates. Recording contacts of different subjects
65 are color-coded. In both **a** and **b**, right hemisphere recording locations are flipped to the left
66 hemisphere: left side contacts are marked with circles, and right side contacts are marked with
67 triangles.

69 Behavioral performance

70 Across all subjects, the mean speech production latency (interval between stimulus presentation
71 and onset of speech) was 1.07 ± 0.29 s, and the mean duration of speech was 0.70 ± 0.09 s.
72 Nonword production latency (1.23 ± 0.37 s) was significantly longer than word production latency
73 (0.98 ± 0.24 s) across subjects (two-tailed paired t-test, $t(10)=4.47$, $P=0.0012$; Figure 3a).
74 Nonword production duration across subjects (0.68 ± 0.07 s) was not significantly different from
75 word production duration (0.72 ± 0.13 s; two-tailed paired t-test, $t(10)=1.99$, $P=0.074$; Figure 3b).

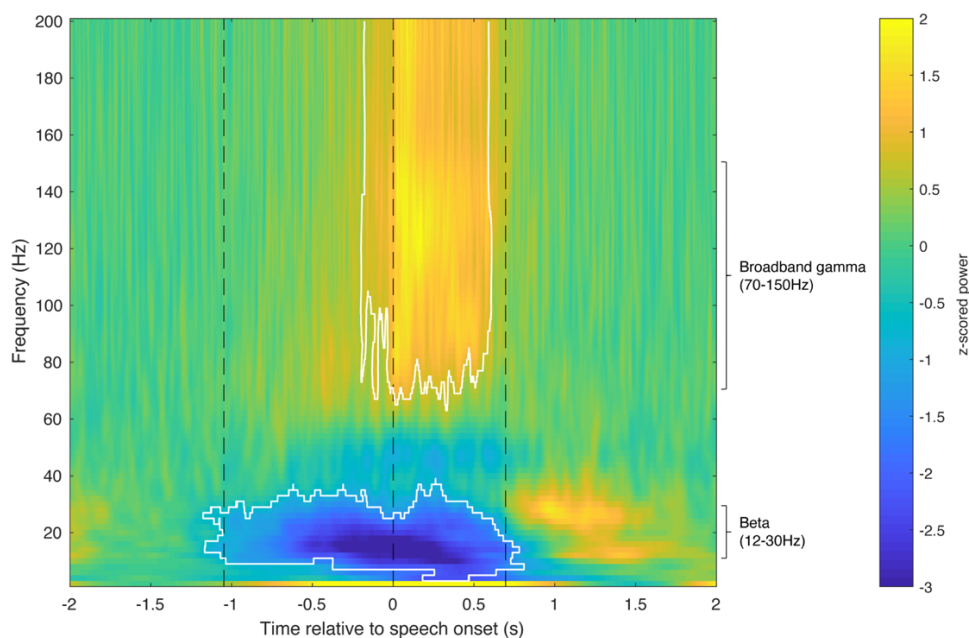


76

77 **Figure 3: Behavioral outcomes.** **a** Mean and SEM of speech production latency for each
78 subject across all trials (first column), word trials (second column), or nonword trials (third
79 column), superimposed with the mean and SEM of speech production latency across subjects.
80 **b** Mean and SEM of speech duration for each subject across all trials (first column), word trials
81 (second column), or nonword trials (third column), superimposed with the mean and SEM of
82 speech duration across subjects. Two-tailed paired t-test, $**P<0.01$, ns: not significant.
83

84 **Thalamic neural activity is modulated during reading aloud**

85 Thalamic LFP activity exhibited significant time-frequency modulation during the reading aloud
86 task (Figure 4). Compared to baseline (a period of 1000ms preceding stimulus presentation),
87 there was a significant decrease in spectral power in the beta frequency band (12-30Hz) that
88 occurred at stimulus presentation and lasted until the end of speech (-1.08-0.62s relative to
89 speech onset, two-tailed Wilcoxon signed-rank test, $n=117$, $P<0.05$, Bonferroni corrected). In
90 contrast, a significant increase in broadband gamma (70-150Hz) activity occurred shortly before
91 the onset of speech and persisted throughout the utterance (-0.15-0.59s relative to speech
92 onset, two-tailed Wilcoxon signed-rank test, $n=117$, $P<0.05$, Bonferroni corrected). Average z-
93 scored task-related beta and broadband gamma response amplitudes of each trial were then
94 calculated over the respective significant time windows for all the recordings. As a result, 66/117
95 (56%) of the recordings showed significant beta activity decreases during the task compared to
96 baseline (one-tailed one-sample t-test, $P<0.05$, Bonferroni corrected), and significant task-
97 related broadband gamma activity increases were observed in 91/117 (78%) of the recordings
98 (one-tailed one-sample t-test, $P<0.05$, Bonferroni corrected).
99

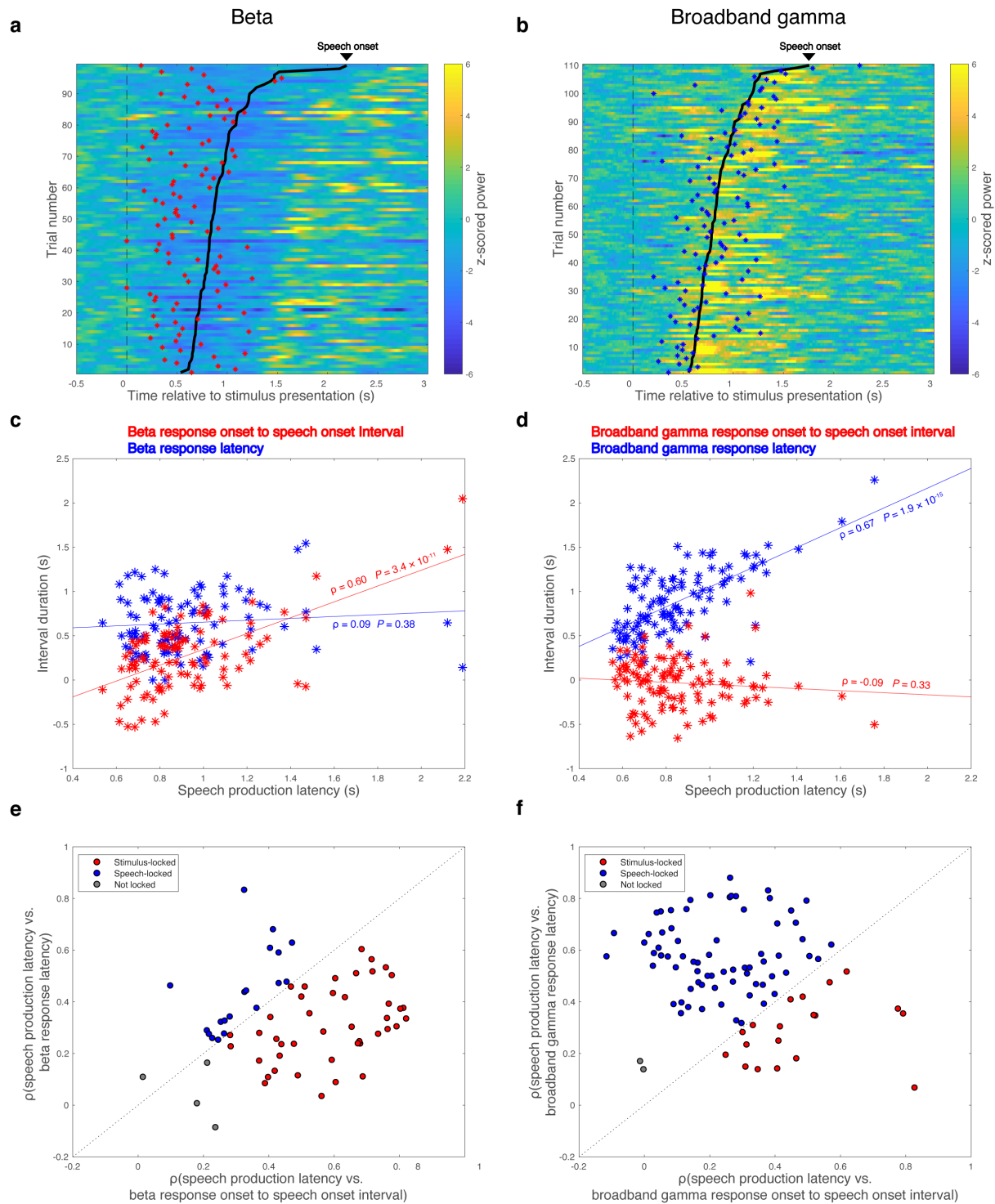


100

101 **Figure 4: Thalamic neural activity shows task-related modulations.** A spectrogram of
102 thalamic neural activity during the reading aloud task, averaged across all trials and all
103 recordings. Trials are aligned to speech onset. Significant changes compared to baseline are
104 marked in white contours (-1.08-0.62s for beta activity, and -0.15-0.59s for broadband gamma
105 activity; Wilcoxon signed-rank test, $n=117$, $P<0.05$, Bonferroni corrected). Average time points
106 of stimulus presentation, speech onset and offset are marked with black dashed lines.
107

108 **Beta and broadband gamma responses differ in timing properties**

109 The average interval between stimulus presentation and onset of a significant change from
110 baseline in the spectral power of a particular frequency band, i.e. the mean band response
111 latency, was shorter for significant beta decrease responses than for significant broadband
112 gamma increase responses (0.79 ± 0.18 s vs. 0.99 ± 0.18 s, two-tailed two-sample t-test, $t(155)=-$
113 6.97 , $P<10^{-5}$). The mean band response onset to speech onset interval was also greater for
114 significant beta decrease responses than for significant broadband gamma increase responses
115 (0.31 ± 0.15 s vs. 0.13 ± 0.14 s, two-tailed two-sample t-test, $t(155)=7.67$, $P<10^{-5}$). To characterize
116 the temporal properties of these responses, we examined their trial-to-trial relationships to
117 stimulus presentation versus speech onset (Figure 5a-d). Of the 66 recordings that showed
118 significant task-related beta power decreases, 43 (65.2%) had beta responses time-locked to
119 stimulus presentation, whereas only 19 (28.8%) had beta responses time-locked to speech
120 onset (Figure 5e). In contrast, the majority (70/91, 77.0%) of significant broadband gamma
121 power increases were time-locked to speech onset, with a minority (19/91, 21.0%) time-locked
122 to stimulus presentation (Figure 5f). These relationships were dissociated (χ^2 test, $\alpha=0.05$;
123 Supplementary Table 1), with beta decreases more likely to be stimulus-locked ($\chi^2(1)=31.4$,
124 $P<10^{-5}$) and broadband gamma increases more likely to be speech onset-locked ($\chi^2(1)=36.1$,
125 $P<10^{-5}$). These temporal correlations did not differ between recording sides (χ^2 test, $\alpha=0.05$;
126 Supplementary Table 2).



127

128 **Figure 5: Beta decrease response is locked to stimulus presentation while broadband**
 129 **gamma increase response is locked to speech onset.** **a, b** Raster plots for beta band
 130 responses (**a**) and broadband gamma responses (**b**) across trials of two representative
 131 recordings. Trials are aligned to stimulus presentation (indicated with black dashed lines) and
 132 sorted by speech production latency. Speech onsets are denoted with bold black lines. Onsets
 133 of significant beta activity decreases are marked with red asterisks in **a** and onsets of significant

134 broadband gamma activity increases are marked with blue asterisks in **b**. **c**, **d** Band response
135 onset to speech onset interval (red asterisks) and band response latency (blue asterisks) are
136 correlated (Pearson's correlation, $\alpha=0.05$) with speech production latency respectively, for the
137 two representative recordings. **e**, **f** The same correlation analysis is performed for all the
138 recordings with significant beta decrease responses and all the recordings with significant
139 broadband gamma increase responses, and the results are summarized in **e** and **f**, respectively.
140 Recordings locked to stimulus presentation are shown in red, recordings locked to speech onset
141 are shown in blue, and recordings not locked to either stimulus presentation or speech onset
142 are shown in gray.

143

144 **Thalamic beta activity is selective to lexical status**

145 To investigate the involvement and lateralization of the thalamus in lexical processing, only
146 recordings that were from subjects with bilateral lead recordings ($n=7$) and that showed
147 significant task-related modulation were included for lexicality-related analyses. As a result, 55
148 recordings (21 unilateral session left-side recordings, 34 from bilateral session left-side (20) and
149 right-side (14) recordings) were included for beta lexical selectivity analysis. Nonword
150 production was associated with a greater suppression of beta power compared with reading
151 words. These differential beta responses were observed in both hemispheres (Figure 6a, c). In
152 the left thalamus, significant word vs. nonword beta amplitude differences occurred between
153 0.8s and 1.8s after stimulus presentation (two-tailed paired t-test, $n=41$, $P<0.05$, Bonferroni
154 corrected). Similarly, significant beta amplitude differences occurred in the right thalamus at 0.2-
155 1.7s relative to stimulus presentation (two-tailed paired t-test, $n=14$, $P<0.05$, Bonferroni
156 corrected).

157

158 To quantify the lexical selectivity of thalamic beta activity, a lexical selectivity index was
159 determined for each of these recordings. We utilized the time window of significant task-related
160 beta activity decrease (-1.08-0.62s relative to speech onset (see Figure 4)) to calculate a mean
161 task-related beta response power value for each trial, and then the values were compared
162 between nonword trials vs. word trials in each recording by performing a two-sample t-test. The
163 resulting t-statistic was the beta lexical selectivity index for this recording: a beta lexical
164 selectivity index less than zero indicated stronger beta activity decrease (thus having more
165 negative z-scored power) during nonword trials than during word trials, and vice versa. The
166 mean beta lexical selectivity indexes for unilateral session left-side recordings (-0.49 ± 0.76),
167 bilateral session left-side (-0.52 ± 0.82) and right-side (-0.82 ± 0.89) recordings were all
168 significantly less than zero (two-tailed one-sample t-test, $t(20)=-2.97$, $P=0.0075$; $t(19)=-2.83$,
169 $P=0.011$; $t(13)=-3.48$, $P=0.0041$; Figure 6e), suggesting that the magnitude of the beta

170 decrease was significantly nonword-selective in each case. There were no significant
171 differences in beta lexical selectivity between recordings in the left and right thalamus, or
172 between recordings from the unilateral and bilateral sessions on the left side (two-tailed two-
173 sample t-test, unilateral session left-side recordings vs. bilateral session right-side recordings:
174 $t(33)=1.18$, $P=0.25$; bilateral session left-side recordings vs. bilateral session right-side
175 recordings: $t(32)=1.05$, $P=0.30$; unilateral session left-side recordings vs. bilateral session left-
176 side recordings: $t(39)=0.093$, $P=0.93$).

177

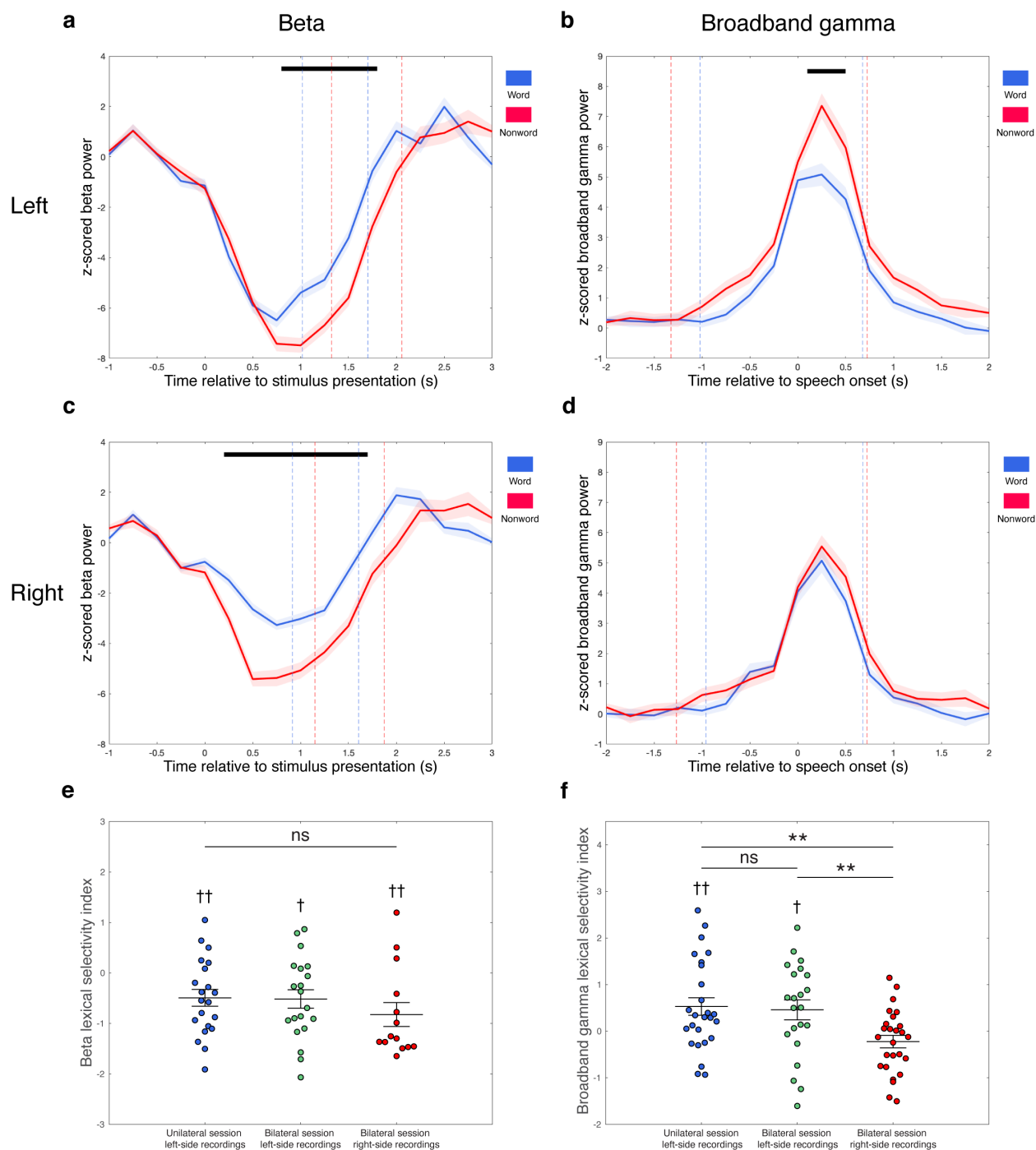
178 **Lexical selectivity of thalamic broadband gamma activity is lateralized**

179 74 recordings (26 unilateral session left-side recordings, 22 bilateral session left-side
180 recordings, and 26 bilateral session right-side recordings) were included for broadband gamma
181 lexical selectivity analysis. Significantly greater broadband gamma activity increases during
182 nonword production were observed in the left thalamus, starting 0.1s after speech onset and
183 persisting throughout the following 0.4s (two-tailed paired t-test, $n=48$, $P<0.05$, Bonferroni
184 corrected; Figure 6b). In the right thalamus, however, the broadband gamma response curves
185 observed during nonword and word reading were similar, without a significant difference in
186 response amplitudes (two-tailed paired t-test, $n=26$, $\alpha=0.05$, Bonferroni corrected; Figure 6d).

187

188 We next calculated broadband gamma lexical selectivity indexes, using the significant time
189 window of -0.15-0.59s relative to speech onset (see Figure 4). A broadband gamma lexical
190 selectivity index greater than zero indicated stronger broadband gamma activity increase during
191 nonword trials than during word trials, and vice versa. The mean broadband gamma lexical
192 selectivity indexes of both unilateral session left-side recordings (0.53 ± 0.96) and bilateral
193 session left-side recordings (0.46 ± 1.00) were significantly greater than zero (two-tailed one-
194 sample t-test, $t(25)=2.80$, $P=0.0097$; $t(21)=2.14$, $P=0.044$), indicating significant correlation of
195 the magnitude of the gamma response to lexical status (Figure 6f). In contrast, broadband
196 gamma responses in right side recordings did not show significant lexical selectivity (-0.22
197 ± 0.68 , two-tailed one-sample t-test, $t(25)=-1.67$, $P=0.11$). The differences in broadband gamma
198 lexical selectivity between the left and right thalamus were demonstrated with two-tailed two-
199 sample t-test (unilateral session left-side recordings vs. bilateral session right-side recordings:
200 $t(50)=3.25$, $P=0.0021$; bilateral session left-side recordings vs. bilateral session right-side
201 recordings: $t(46)=2.79$, $P=0.0077$), further suggesting that selectivity of thalamic broadband
202 gamma activity to lexical status is lateralized to the left. Recordings in the unilateral and bilateral
203 sessions on the left side did not differ in broadband gamma lexical selectivity (two-tailed two-

204 sample t-test, $t(46)=0.25$, $P=0.80$), indicating the consistency of broadband gamma lexical
 205 selectivity between task sessions.



206
 207 **Figure 6: Differential band responses during word vs. nonword reading aloud in the left**
 208 **and right thalamus. a-d** Comparisons of average band response amplitudes during word (blue)
 209 vs. nonword (red) reading aloud for beta band (**a, c**) and broadband gamma (**b, d**), in the left (**a,**
 210 **b**) and right thalamus (**c, d**). Band responses are averaged across trials of respective trial types
 211 and across recordings that showed significant task-related band responses in each side, aligned

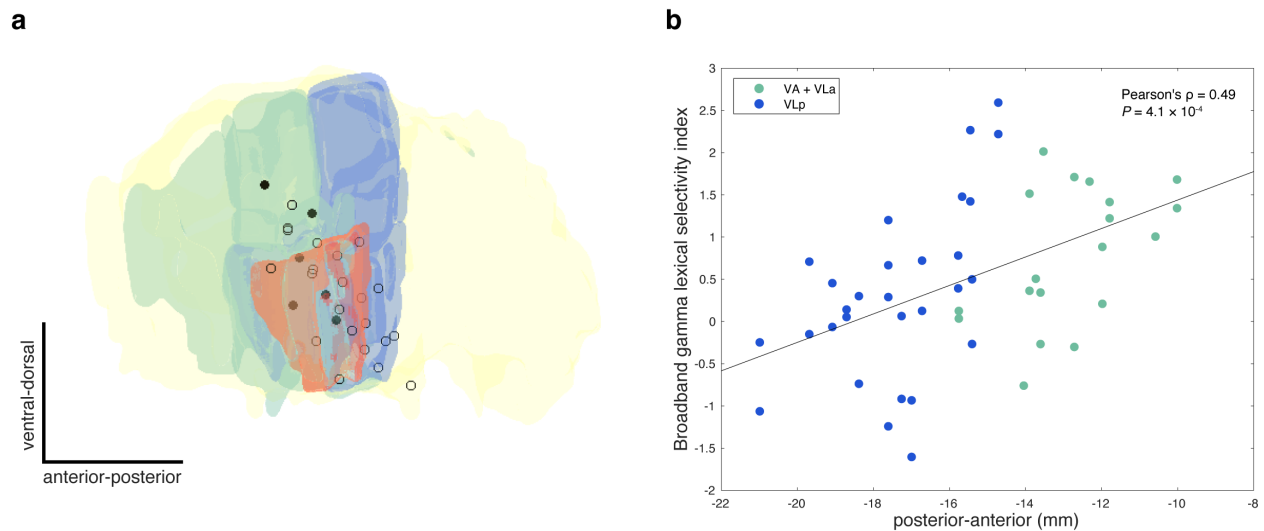
212 to stimulus presentation for beta band (**a, c**) and speech onset for broadband gamma (**b, d**).
213 Average time points of speech onset and end of speech are marked with dashed lines in **a** and
214 **c**, and average time points of stimulus presentation and end of speech are marked with dashed
215 lines in **b** and **d**, for word trials (blue) and nonword trials (red) respectively. Black bars indicate
216 significant differences of response amplitudes between word and nonword trials (two-tailed
217 paired t-test, $P < 0.05$, Bonferroni corrected). Standard errors are shaded in light colors. **e** Dot
218 plot of beta lexical selectivity indexes of lead recordings that showed significant task-related
219 beta decrease responses, grouped by recording sides and recording sessions (unilateral
220 session left-side recordings in the first column, bilateral session left-side recordings in the
221 second column, and bilateral session right-side recordings in the third column). Mean and SEM
222 of beta lexical selectivity index across recordings of each group is superimposed on each
223 column, respectively. **f** Dot plot of broadband gamma lexical selectivity indexes of lead
224 recordings that had significant task-related broadband gamma increase responses, grouped by
225 recording sides and recording sessions (unilateral session left-side recordings in the first
226 column, bilateral session left-side recordings in the second column, and bilateral session right-
227 side recordings in the third column). Mean and SEM of broadband gamma lexical selectivity
228 index across recordings of each group is superimposed on each column, respectively. Two-
229 tailed one-sample t-test, $\dagger P < 0.05$, $\dagger\dagger P < 0.01$; two-tailed two-sample t-test, $**P < 0.01$, ns: not
230 significant.

231

232 **Left side broadband gamma lexical selectivity is topographically organized**

233 We observed that the recording sites in the left thalamus that were significantly nonword-
234 selective in terms of broadband gamma response activity (broadband gamma lexical selectivity
235 index > 1.645 based on normal approximation of t-distribution) appeared to comprise more
236 anterior locations in MNI space (Figure 7a). Pearson's correlation tests demonstrated that the
237 broadband gamma lexical selectivity index significantly correlated with recording location along
238 the anterior-posterior axis (MNI-defined y coordinate; $n=48$, $\rho=0.49$, $P=0.00041$; Figure 7b) and
239 the ventral-dorsal axis (MNI-defined z coordinate; $n=48$, $\rho=0.30$, $P=0.041$; Supplementary
240 Figure 1a), but not the lateral-medial axis (MNI-defined x coordinate; $n=48$, $\rho=-0.14$, $P=0.34$;
241 Supplementary Figure 1b) within the left thalamus. To avoid multicollinearity and to test out
242 possible interactions between variables, a stepwise linear regression model was applied, which
243 determined that the anterior-posterior location of the recording was the only significant predictor
244 (estimated coefficient=0.17, SE=0.044, $P=0.00041$), while neither the ventral-dorsal location
245 ($P=0.72$) nor the interaction between ventral-dorsal location and anterior-posterior location
246 ($P=0.14$) explained the result. In order to control for subject differences and session differences,
247 we further fitted linear mixed effects models to the data, entering subject and session as random
248 effects. The results indicate that even after accounting for subject and session variability, the
249 broadband gamma lexical selectivity index in the left thalamus had a significant gradient along

250 the anterior-posterior axis, with greater broadband gamma lexical selectivity index more likely to
251 be observed anteriorly (estimated coefficient=0.17, SE=0.043, $P=0.00032$). Based on the linear
252 mixed effects modeling results, neither ventral-dorsal location (estimated coefficient=0.061,
253 SE=0.035, $P=0.087$) nor lateral-medial location (estimated coefficient=-0.11, SE=0.093, $P=0.24$)
254 of the recording had significant effect on broadband gamma lexical selectivity in the left
255 thalamus. Taken together, these results suggest that broadband gamma lexical selectivity is
256 dependent on the anterior-posterior location of the recording in the left ventral lateral thalamus,
257 with greater nonword selectivity more likely to occur anteriorly.



258

259 **Figure 7: Broadband gamma lexical selectivity depends on anterior-posterior location of**
260 **the recording in the left thalamus. a** Left side lead recording sites are plotted together with
261 anatomical structures (thalamus in yellow, VA and VLc in green, VLp in blue, and Vim in
262 orange), viewed from a lateral direction. Recording sites where significantly nonword-selective
263 recordings in terms of broadband gamma response amplitudes (broadband gamma lexical
264 selectivity index > 1.645 based on normal approximation of t-distribution) were observed in either
265 session are filled with black, and remaining recording sites are shown in open circles. **b**
266 Broadband gamma lexical selectivity indexes of left side lead recordings that showed significant
267 task-related broadband gamma responses are correlated (Pearson's correlation, $\alpha=0.05$) with
268 recording locations along the anterior-posterior axis (y coordinates in MNI space). Recordings
269 inside VA or VLc are green-colored and recordings inside VLp are blue-colored.

270

271 No significant correlation (Pearson's correlation, $\alpha=0.05$) between broadband gamma lexical
272 selectivity index and recording location was observed for right side recordings (Supplementary
273 Figure 2 and 3), or for beta lexical selectivity on either side (Supplementary Figure 4 and 5), by
274 any statistical modeling. These results suggest that the topography of lexical selectivity is
275 unique to broadband gamma responses in the left thalamus.

276

277 **Discussion**

278 Subcortical contributions to language production have been hypothesized largely from
279 correlations of focal brain damage with aphasic syndromes and from language studies using
280 functional magnetic resonance imaging (fMRI) or scalp electroencephalography (EEG) (Hebb &
281 Ojemann, 2013). Our results are the first to demonstrate thalamic neural activity during reading
282 aloud. We discovered that the encoding of lexical status is differentially represented in thalamic
283 neural activity. Whereas greater beta activity decrease occurred during nonword trials as
284 compared to word trials in both hemispheres, greater gamma increases in the left but not right
285 thalamus were associated with the spoken production of nonwords as compared to words.
286 Importantly, the level of broadband gamma lexical selectivity was greater in more anterior
287 thalamic recording locations, regions more likely to receive basal ganglia than cerebellar
288 afferents (Alexander et al., 1986).

289
290 We first observed that thalamic beta activity showed a task-related decrease, locked to stimulus
291 presentation, consistent with the expected beta desynchronization that accompanies motor
292 action. Beta oscillations are proposed to signal the maintenance of current sensorimotor and
293 cognitive states (Engel & Fries, 2010), and event-related beta activity decreases during the
294 preparation and the execution of voluntary movements have been observed across relevant
295 brain regions, including the thalamus (Klostermann et al., 2007; Kühn et al., 2004; Paradiso,
296 2004; Tzagarakis et al., 2010). Beta activity was reduced across the entirety of each task event,
297 which requires a series of underlying neural dynamics (processing the visual stimulus, retrieval
298 of lexical information, encoding of the phonological information, and execution of articulatory
299 movement), suggesting a state change that facilitated the process of speech production.
300 Significant increases in broadband gamma activity began before but were predominantly locked
301 to speech onset. Given that broadband gamma activity is thought to index synchronized local
302 neuronal firing (Ray et al., 2008; Ray & Maunsell, 2011) and is associated with the functional
303 activation of relevant brain regions during a wide range of sensorimotor and cognitive tasks,
304 including speech and language processing (Bouchard et al., 2013; Chrabaszcz et al., 2019;
305 Crone et al., 2006; Juphard et al., 2011; Uhlhaas et al., 2011), our data suggest that the ventral
306 lateral thalamus tracks speech production.

307
308 Studies of the brain networks involved in lexical processing during reading primarily have been
309 confined to cortical regions (Dietz et al., 2005; Fiez et al., 1999; Hagoort et al., 1999; Heim et
310 al., 2005; Herbster et al., 1997; Juphard et al., 2011; Mechelli et al., 2003; Xu, 2001). In this

311 study, we utilized the balanced design of words and nonwords in the stimulus sets and
312 simultaneous bilateral recordings in the seven participants to determine whether lexical
313 processing is differentially represented in the thalamus during reading aloud. Thalamic
314 broadband gamma oscillations showed significantly stronger activation during nonword reading
315 aloud than during word reading aloud, which evolved around speech onset and was present
316 throughout the entire utterance. Notably, this broadband gamma lexical selectivity was found
317 only in recordings from the left side. According to classic speech production models (Levelt et
318 al., 1999), the time course of the observed broadband gamma activity difference between word
319 and nonword trials corresponded to the articulatory stage of reading aloud. It is unlikely that this
320 lexicality effect was motoric, considering that the motor complexity was balanced between word
321 and nonword stimuli, and that this differential broadband gamma modulation was not
322 equivalently observed in the right hemisphere. In fact, the dual-route theory of reading aloud has
323 suggested that words and nonwords are read aloud differently: while real words can be read
324 aloud via either grapheme-to-phoneme conversions or direct word-to-sound mapping, nonwords
325 can only be read aloud via grapheme-to-phoneme conversions (Coltheart et al., 2001). It is
326 possible that phonological encoding was still ongoing during nonword production, after a failed
327 internal lexicon lookup procedure. Indeed, stronger gamma (50-150Hz) responses for pseudo-
328 words than for words have been reported in Broca's area (Brodmann's areas 44 and 45) during
329 silent word reading, where the length of this differential response increased with the length of
330 the stimuli (Juphard et al., 2011). In addition, it is possible that reading aloud nonwords created
331 a learning or error correction demand (Hickok, 2014). We propose that the lexicality effect on
332 thalamic broadband gamma activity during reading may reflect left thalamic participation in
333 phonological encoding, learning, and feedback monitoring during speech and language
334 processing. Although previous studies have supported a lateralized thalamic role in language
335 (Johnson & Ojemann, 2000), our results from simultaneous bilateral direct recordings in the
336 thalamus are the first to provide direct supporting evidence.

337
338 A topography for broadband gamma lexical selectivity was observed in the left thalamus. The
339 lexical selectivity of the broadband gamma response was significantly correlated with the
340 anterior-posterior location of recording sites in the left thalamus, with a higher lexical selectivity
341 more likely to appear anteriorly. In contrast, a gradient for broadband gamma lexical selectivity
342 was not observed in the right thalamus. This finding further supports a unique language role
343 lateralized to the left thalamus, and suggests functional heterogeneity in the left ventral lateral
344 thalamus during speech and language processing. The anterior portion (VA and VLa) receives

345 input primarily from the internal globus pallidus and substantia nigra pars reticulata, and has
346 strong connections with frontal cortex, including Broca's area (Alexander et al., 1986; Behrens
347 et al., 2003; Bosch-Bouju et al., 2013; Hintzen et al., 2018; Hwang et al., 2017; Zhang et al.,
348 2010). Broca's area has consistently been associated with lexico-phonological processing (Dietz
349 et al., 2005; Fiez et al., 1999; Hagoort et al., 1999; Heim et al., 2005; Herberster et al., 1997;
350 Juphard et al., 2011; Mechelli et al., 2003; Xu, 2001). Thus, this thalamic region may participate
351 in differential lexical processing during nonword vs. word reading aloud in concert with Broca's
352 area. In contrast, the posterior region (VLp), which receives cerebellar projections and
353 preferentially sends output to primary motor cortex (Behrens et al., 2003; Bosch-Bouju et al.,
354 2013; Hintzen et al., 2018; Hwang et al., 2017; Zhang et al., 2010), might be more related to
355 motor control of a selected motor plan. This idea is supported by previous stimulation studies
356 that have reported location-dependent effects of thalamic stimulation on speech and language:
357 stimulation of VLa could cause acceleration of language processes, while stimulation of VLp
358 often affected motor aspects of speech, such as perseveration and stuttering speech (Hebb &
359 Ojemann, 2013). We note that VA has been proposed to participate in selection of a language
360 unit during speech production, via basal ganglia-thalamo-cortical loop interactions (Crosson,
361 2013); it also is included in the "planning loop" in the GODIVA model of speech production
362 (Bohland et al., 2010).

363
364 In contrast, although significantly stronger nonword-related than word-related beta activity
365 decreases accompanied the reading aloud task bilaterally, neither lateralization nor topography
366 was observed for thalamic beta lexical selectivity. Therefore, beta activity decreases likely
367 represent nonspecific changes of cognitive and sensorimotor states that prepare the entire
368 thalamo-cortical network for a behavioral change. Note that in the current work we did not try to
369 compare task-related band response strength between different recording locations and
370 different recording sides among subjects and sessions, because of a number of uncontrollable
371 factors that affect the band oscillatory power (e.g. recording impedances and baseline neural
372 activity are variable across subjects, sessions, and recording sides). In contrast, the lexical
373 selectivity index, which was calculated by comparing word-related and nonword-related band
374 response strength within each recording, is mostly independent of those factors and thus
375 comparable at the group level. This idea is supported by the fact that lexical selectivity indexes
376 in both beta and broadband gamma bands remained consistent across sessions.

377

378 In summary, our results are the first demonstration of time-frequency modulations of thalamic
379 neural activity during reading aloud. These data suggest that lateralized and topographically
380 organized thalamic pathways participate in speech production differently, based on whether a
381 word or nonword is being read.

382

383 **Materials and methods**

384 **Subjects**

385 Eleven human subjects (3 females, 68.4 ±8.0 years) with essential tremor undergoing awake
386 DBS implantation surgery targeting the Vim nucleus of the thalamus were studied. All
387 participants were right-handed native English speakers. None had significant cognitive
388 impairment based on a detailed neuropsychological evaluation performed during clinical
389 evaluation for DBS surgery. All but one underwent bilateral (left side first) DBS lead implantation
390 (one subject had one lead implanted in the left hemisphere previously and underwent right side
391 lead implantation in the current study). Full demographic description of subjects is provided in
392 Table 1. All protocols were approved by the Institutional Review Board of the University of
393 Pittsburgh (IRB Protocol #PRO13110420), and all participants gave written informed consent.

394 **Table 1: Subject characteristics.**

| Subject | Age | Gender | Handedness | MMSE | LFP recording side | LFP recording type | Number of recordings | Mean number of trials per session | Trials rejected, % |
|---------|-----|--------|------------|-------|--------------------|--------------------|----------------------|-----------------------------------|--------------------|
| 1 | 61 | Male | Right | NR | Left | Mapping electrodes | 12 | 111 | 7 |
| 2 | 70 | Female | Right | 30/30 | Right | Mapping electrodes | 6 | 107 | 11 |
| 3 | 66 | Male | Right | NR | Left | Mapping electrodes | 6 | 116 | 3 |
| 4 | 75 | Male | Right | 26/30 | Left | Mapping electrodes | 9 | 112 | 5 |
| 5 | 64 | Male | Right | 30/30 | Both | DBS leads | 12 | 104 | 13 |
| 6 | 53 | Male | Right | NR | Both | DBS leads | 12 | 113 | 5 |
| 7 | 67 | Male | Right | 26/30 | Both | DBS leads | 12 | 111 | 7 |
| 8 | 71 | Male | Right | 26/30 | Both | DBS leads | 12 | 108 | 9 |
| 9 | 84 | Female | Right | 30/30 | Both | DBS leads | 12 | 118 | 2 |
| 10 | 73 | Female | Right | 30/30 | Both | DBS leads | 12 | 109 | 9 |
| 11 | 68 | Male | Right | 28/30 | Both | DBS leads | 12 | 114 | 5 |

395 MMSE: Mini-Mental State Examination; NR: not recorded.

396

397 **Stimuli and experimental paradigm**

398 Subjects performed a reading aloud task either in the course of subcortical mapping procedure
 399 during the surgery (4/11 subjects with mapping electrode recordings) or after the placement of
 400 DBS lead in each side (7/11 subjects with lead electrode recordings). For the 4 subjects with
 401 mapping electrode recordings, each subject performed up to 4 task sessions, while the 7
 402 subjects with lead electrode recordings each performed 2 task sessions (the first session
 403 occurred after left lead was implanted, and the second session took place after bilateral
 404 implantation was completed). Each session included 120 trials. The stimuli were consonant-
 405 vowel-consonant (CVC) words and nonwords that were presented on a computer screen. Four
 406 lists of 120 stimuli (Supplementary Table 3) were constructed based on a previous work (Moore
 407 et al., 2017). The first 60 stimuli of each list alternated between unique words and nonwords,
 408 and those words and nonwords were balanced along a number of psycholinguistic features,
 409 including phoneme probability, phonological neighborhood density, bigram frequency, and

410 biphone probability (see Supplementary Table 4 for the results of statistical comparisons (two-
411 tailed two-sample t-test, $n=60$, $\alpha=0.05$) between the two conditions in terms of these
412 psycholinguistic parameters, which were calculated using the English Lexicon Project database
413 (Balota et al., 2007)). The nonwords were duplicated twice to construct the last 60 stimuli of
414 each list. One of the four stimulus lists was presented to the subjects during each task session.
415 For lexicality-related analyses, only the first 60 trials of each session were used.

416
417 The experimental paradigm was programmed using MATLAB (MathWorks, Natick, MA) and
418 Psychophysics Toolbox extensions (Brainard, 1997). A schematic of the experiment is shown in
419 Figure 1. Before each trial, a white fixation cross was presented on the screen. Each trial was
420 initiated manually by the experimenter, with the appearance of a green fixation cross on the
421 screen. The green fixation cross lasted 250ms, and was followed by a variable time delay (500-
422 1000ms) during which the screen remained black. Then the CVC syllable stimulus was
423 presented in white on the screen, and subjects were instructed to read it aloud. The text
424 remained on the screen until the subjects finished speaking. A white fixation cross was
425 presented on the screen during the inter-trial interval (ITI).

426

427 **Electrophysiological recordings**

428 For the 4/11 subjects where physiological subcortical mapping was administered, LFP
429 recordings were performed using the Neuro-Omega recording system (Alpha Omega, Nazareth,
430 Israel) and mapping electrodes that have a stainless steel macroelectrode ring (0.55mm in
431 diameter, 1.4mm in length) 3mm above the tip, while in the other 7/11 subjects LFP signal was
432 recorded from Medtronic Model 3387 DBS leads (Medtronic, Minneapolis, MN) with four
433 platinum-iridium electrodes (1.27mm in diameter, 1.5mm in length) that are spaced 1.5mm
434 apart, using Grapevine Neural Interface Processor (Ripple LLC, Salt Lake City, UT). The
435 mapping electrodes and the DBS leads targeted the Vim. For subjects with mapping electrode
436 recordings, three mapping electrodes were placed in three trajectories (anterior, central, and
437 posterior or central, posterior, and medial) of a standard cross-shaped Ben-Gun array with a
438 2mm center-to-center spacing, and made simultaneous recordings starting at 15mm above the
439 surgical target with manual advance in 0.1mm steps. The reading aloud task was carried out in
440 pauses during subcortical mapping procedure and subjects performed in up to four recording
441 sessions, with each session corresponding to a different recording depth. Mapping electrode
442 recordings were performed only during the left side implantation except for one subject who
443 underwent unilateral implantation in the right side, and thus got mapping electrode recordings

444 only in the right side. For subjects with DBS lead electrode recordings, the task was
445 administered in two recording sessions, one after the implantation of the DBS lead in the left
446 side, receiving recordings from only the left DBS lead electrodes, and the other after bilateral
447 DBS lead implantation was completed, receiving simultaneous recordings from bilateral lead
448 electrodes. The LFP signal recorded from mapping electrodes was sampled at 44kHz and
449 bandpass filtered from 0.075Hz to 10kHz, and data recorded from DBS lead electrodes were
450 collected at 30kHz. Signal collected in one recording site in one session counted as one
451 recording. Subject recording characteristics are summarized in Table 1.

452

453 **Audio recordings**

454 Subjects' speech signal was recorded using an omnidirectional microphone (Audio-Technica
455 model ATR3350iS Mic, frequency response 50-18,000Hz (Audio-Technica, Machida, Japan) for
456 6 subjects, and PreSonus model PRM1 Precision Flat Frequency Mic, frequency response 20-
457 20,000Hz (PreSonus, Baton Rouge, LA) for 5 subjects) placed approximately 8cm away from
458 the subject's mouth and oriented at an angle of about 45°. The audio signal was collected by
459 Grapevine Neural Interface Processor at a sampling frequency of 30kHz. For subjects with
460 mapping electrode recordings, the audio signal was then synchronized with neural signal
461 recorded by the Neuro-Omega system using digital pulses delivered to both recording systems
462 via a USB data acquisition unit (model USB-1208FS, Measurement Computing, Norton, MA).

463

464 **Electrode localization**

465 DBS lead electrodes and mapping electrodes were localized using LEAD-DBS toolbox (Horn et
466 al., 2019; Horn & Kühn, 2015). Postoperative brain scans were coregistered to preoperative
467 brain scans using open-source Advanced Normalization Tools (ANTs). Pre- and postoperative
468 acquisitions were then normalized into MNI ICBM152 NLIN 2009b stereotactic space (Fonov et
469 al., 2011). Both coregistration and normalization results underwent manual quality check. Semi-
470 automatic reconstruction of electrodes in MNI space was performed in LEAD-DBS and MNI-
471 defined coordinates were determined for all the electrode contacts (Figure 2). A digitized and
472 normalized to MNI space version of the Ewert atlas (Ewert et al., 2018) was used to categorize
473 the electrode contacts. A contact was assigned to a nucleus if it was within or in the vicinity of
474 the nucleus (1mm cut-off) based on the minimum Euclidean distance between the contact and
475 the voxels of the nucleus.

476

477 **Data pre-processing**

478 The audio signal was segmented into trials and the speech sound was coded by communication
479 science students trained in phonetics in a custom-designed graphical user interface
480 implemented in MATLAB. The coding results were manually checked by a speech-language
481 pathologist. For each trial, (1) the onset of speech was identified, (2) the end of speech was
482 identified, and (3) the speech content was identified. Trials were considered to have correct
483 speech responses and were included in further analyses if they met all the following criteria: (1)
484 the subject's speech response could be clearly identified by the coder, (2) the subject's
485 response was a CVC syllable consisting of the targeted phonemes, and (3) the response did not
486 make nonword into a word or word into a nonword.

487

488 Electrophysiological data were pre-processed using custom code based on FieldTrip toolbox
489 (Oostenveld et al., 2011) in MATLAB. The data were resampled at 1kHz and band-pass filtered
490 from 2 to 400Hz. The data were also notch-filtered at 60Hz and its' harmonics to remove line
491 noise. Time series data from all recording sites were visually and quantitatively inspected for
492 quality control. The data were then segmented into trials, each spanning 2s before stimulus
493 presentation to 2s after the end of speech. Trials with artefacts or excessive noise were
494 identified both manually and quantitatively, and were excluded for subsequent analyses.

495 Combined with trials that did not meet the criteria for correct speech responses, an average 6.9
496 \pm 3.4% of trials per subject were rejected (Table 1). The remaining data were common-average
497 referenced to minimize noise. For spectral-temporal analysis, the data were decomposed using
498 Morlet wavelet transformation (width=7) over frequencies of 2Hz to 200Hz in increment steps of
499 2Hz. For band activity analyses, instantaneous analytic amplitudes of beta and broadband
500 gamma frequency bands were extracted from respective bandpass filters using Hilbert
501 transform (MATLAB function *hilbert*). The resulting signal of each trial was z-scored relative to
502 the baseline (a period of 1000ms preceding stimulus presentation).

503

504 **Task-related responses**

505 Time-frequency data were averaged across all trials centering on speech onset (from 2s before
506 speech onset to 2s after speech onset), z-scored to baseline, and then averaged across all
507 recordings. Nonparametric two-tailed Wilcoxon signed-rank test was performed to determine
508 significant time-frequency modulations compared to baseline ($n=117$, $\alpha=0.05$, Bonferroni
509 corrected). Significant time windows for beta and broadband gamma determined by the
510 statistical results were used to calculate a mean beta response strength and mean broadband
511 gamma response strength for each trial in each recording. Then one-tailed one-sample t-test

512 was performed on each recording to determine recordings that had significant beta activity
513 decreases and recordings that had significant broadband gamma activity increases, respectively
514 ($\alpha=0.05$, Bonferroni corrected).

515

516 **Locking analysis**

517 In an effort to characterize the timing properties of beta decrease response and broadband
518 gamma increase response for recordings with significant task-related changes in either band
519 activity, we examined the trial-to-trial relationships of significant band response onsets to
520 stimulus presentation versus speech onset in these recordings. First, beta or broadband gamma
521 time series data of each trial were smoothed using a moving average kernel of 200ms (MATLAB
522 function *smoothdata*) and z-scored to baseline, in order to minimize single-trial noise. For
523 recordings with significant beta decrease responses, a thresholding method with a critical value
524 of $z=-1.645$ was applied to determine the onset of beta response for each trial. Specifically, for
525 each trial, the period with band response power below the threshold that gave minimum
526 summed activity was considered as activation period and the beginning of the period was
527 determined as onset of beta response. For recordings with significant broadband gamma
528 increase responses, the onset of broadband gamma increase was determined in a similar way,
529 except that a critical value of $z=1.645$ was used and period of maximum summed activity above
530 the threshold was considered as activation period. For each band, a trial of one recording was
531 discarded for locking analysis if no beyond-threshold period was present throughout the trial.
532 Two intervals were calculated for each trial: (1) the interval between stimulus presentation and
533 the onset of significant band response (band response latency), and (2) the interval between the
534 onset of significant band response and the onset of speech. Then the two intervals were
535 correlated (Pearson's correlation, $\alpha=0.05$) with speech production latency (interval between
536 stimulus presentation and onset of speech) across trials for each recording, respectively. The
537 band response of a recording was considered to be more time-locked to stimulus presentation,
538 if (1) band response onset to speech onset interval was significantly correlated with speech
539 production latency, and (2) the correlation coefficient (Pearson's ρ) between band response
540 onset to speech onset interval and speech production latency was greater than the correlation
541 coefficient between band response latency and speech production latency. On the contrary, the
542 band response was considered to be more time-locked to speech onset, if (1) band response
543 latency was significantly correlated with speech production latency, and (2) the correlation
544 coefficient between band response latency and speech production latency was greater than the
545 correlation coefficient between band response onset to speech onset interval and speech

546 production latency. If a band response did not meet any of the two criteria, it was considered not
547 locked to either stimulus presentation or speech onset. χ^2 tests were performed to differentiate
548 the locking properties of broadband gamma increase response and beta decrease response,
549 and to test if the locking properties differed between recording sides ($\alpha=0.05$).

550

551 **Lexical selectivity analysis**

552 We utilized the first 60 trials of recordings that were from the seven subjects with bilateral data
553 and that showed significant task-related modulations in beta or broadband gamma activity to
554 make comparisons between the left and right thalamus in terms of band lexical selectivity. A
555 mean z-scored band response curve averaged across trials and across recordings was
556 obtained for each frequency band, each trial type (word/nonword), in each side. Trials were
557 aligned to stimulus presentation for beta and aligned to speech onset for broadband gamma,
558 based on their respective locking properties. Periods of significant differences between word-
559 related responses and nonword-related responses were determined with two-tailed paired t-test
560 using a sliding window of 100ms ($\alpha=0.05$, Bonferroni corrected).

561

562 To quantify the extent of band response difference between word and nonword trials, beta
563 lexical selectivity indexes and broadband gamma lexical selectivity indexes were calculated for
564 respective recordings. For each recording, the mean response power values of a particular
565 frequency band over the corresponding significant time window determined before (see **Task-**
566 **related responses**) were calculated for word trials and nonword trials. Two-sample t-test was
567 then performed between nonword-related power values and word-related power values, and the
568 resulting t-statistic was the lexical selectivity index of that frequency band for that recording. For
569 beta, a lexical selectivity index smaller than zero meant that the recording showed stronger beta
570 activity decrease (thus having more negative z-scored power) during nonword trials than during
571 word trials, and vice versa. For broadband gamma, a lexical selectivity index greater than zero
572 indicated that the recording showed stronger broadband gamma activity increase during
573 nonword reading aloud than during word reading aloud, and vice versa. The beta or broadband
574 gamma activity of a recording was considered significantly nonword-selective, if lexical
575 selectivity index was smaller than -1.645 for beta or greater than 1.645 for broadband gamma
576 (normal approximation of t-distribution). Two-tailed one-sample t-test was performed to test if
577 lexical selectivity indexes of a selected group of recordings were significantly different from zero
578 ($\alpha=0.05$). Two-tailed two-sample t-test was performed to test if lexical selectivity indexes
579 significantly differed between two groups of recordings ($\alpha=0.05$).

580

581 **Analysis of location dependency of lexical selectivity**

582 We further sought to examine possible dependence of band lexical selectivity on recording
583 location, for both beta band and broadband gamma and in both left and right recording sides.
584 Several regression models were applied to the data. First, simple linear regression (Pearson's
585 correlation, $\alpha=0.05$) was performed to correlate lexical selectivity index with recording location:
586 anterior-posterior location (MNI-defined y coordinate), ventral-dorsal location (MNI-defined z
587 coordinate), and lateral-medial location (MNI-defined x coordinate), respectively. A series of
588 stepwise linear regression models (MATLAB function *stepwiselm*, response variable: lexical
589 selectivity index, predictor variables: MNI-defined x, y, z coordinates and their interactions,
590 $\alpha=0.05$) were then carried out to test out possible variable interactions, minimize
591 multicollinearity, and determine the final location dependency model of band lexical selectivity.
592 Finally, in order to account for possible lexical selectivity differences that might exist due to
593 subject- and session-specific variations, linear mixed effects models (MATLAB function *fitglme*)
594 were also applied to the data, setting subject and session as random effects.

595

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601

602 **Competing interests**

603 The authors declare no competing interests.

604

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759 **Thalamic encoding of lexical status is lateralized during reading aloud**

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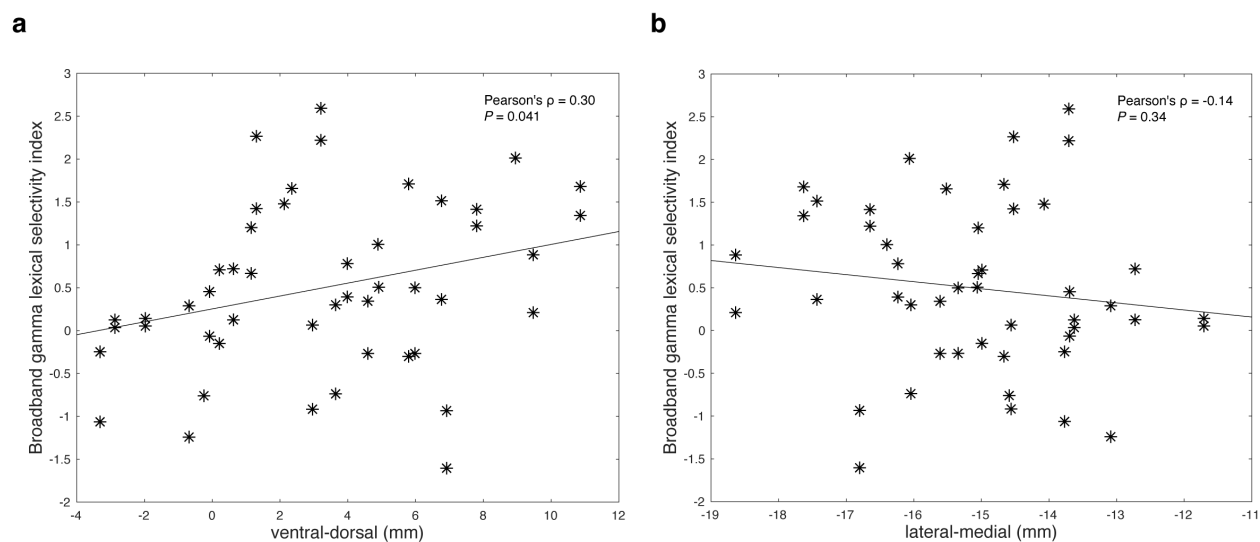
Wang et al., 2020

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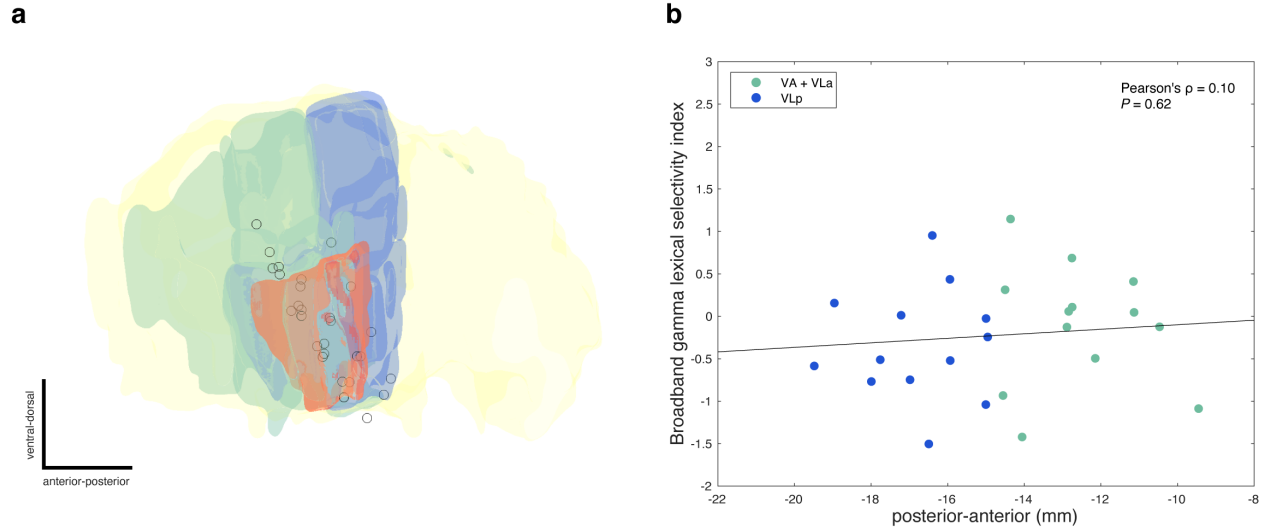
Supplementary Information



766

767 **Supplementary Figure 1: Correlation between left thalamic broadband gamma lexical**
768 **selectivity and recording locations along ventral-dorsal and lateral-medial axes.**

769 Broadband gamma lexical selectivity indexes of left side lead recordings that showed significant
770 task-related broadband gamma increase responses are correlated (Pearson's correlation,
771 $\alpha=0.05$) with ventral-dorsal locations (**a**) and lateral-medial locations (**b**) of the recordings,
772 respectively.

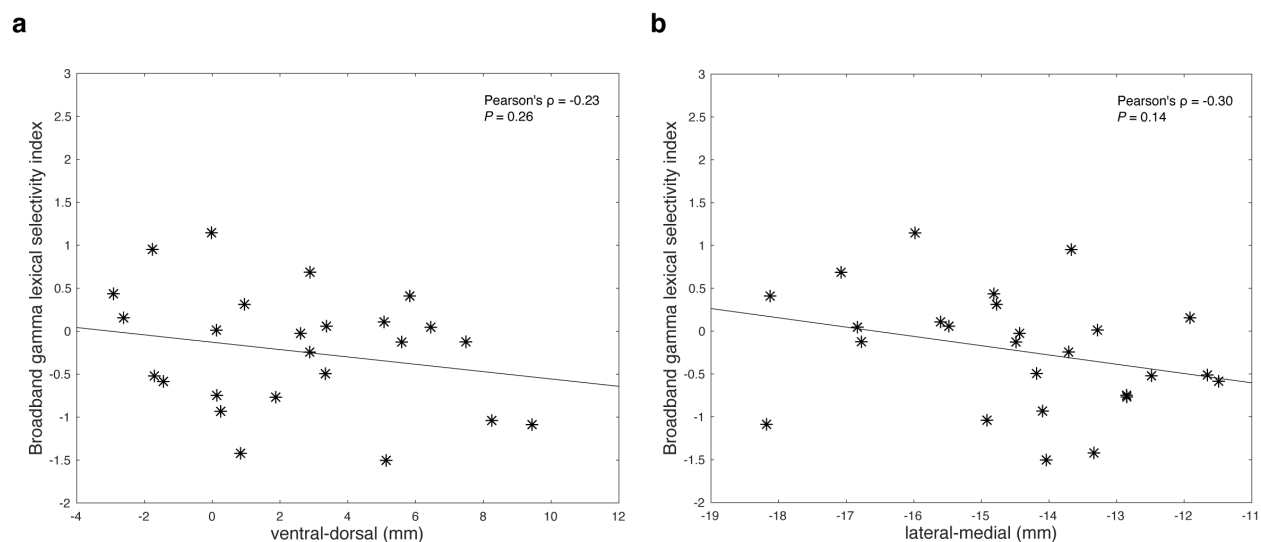


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774 **Supplementary Figure 2: Broadband gamma lexical selectivity does not depend on**
775 **anterior-posterior location of the recording in the right thalamus. a** Right side lead
776 recording sites are flipped to the left and plotted together with anatomical structures (thalamus
777 in yellow, VA and VLa in green, VLp in blue, and Vim in orange), viewed from a lateral direction.
778 Recording sites where significantly nonword-selective recordings in terms of broadband gamma
779 response amplitudes (broadband gamma lexical selectivity index > 1.645 based on normal
780 approximation of t-distribution) were observed are filled with black (n=0), and remaining
781 recording sites are shown in open circles. **b** Broadband gamma lexical selectivity indexes of
782 right side lead recordings that showed significant task-related broadband gamma increase
783 responses are correlated (Pearson's correlation, $\alpha=0.05$) with recording locations along the
784 anterior-posterior axis. Recordings inside VA or VLa are green-colored and recordings inside
785 VLp are blue-colored.

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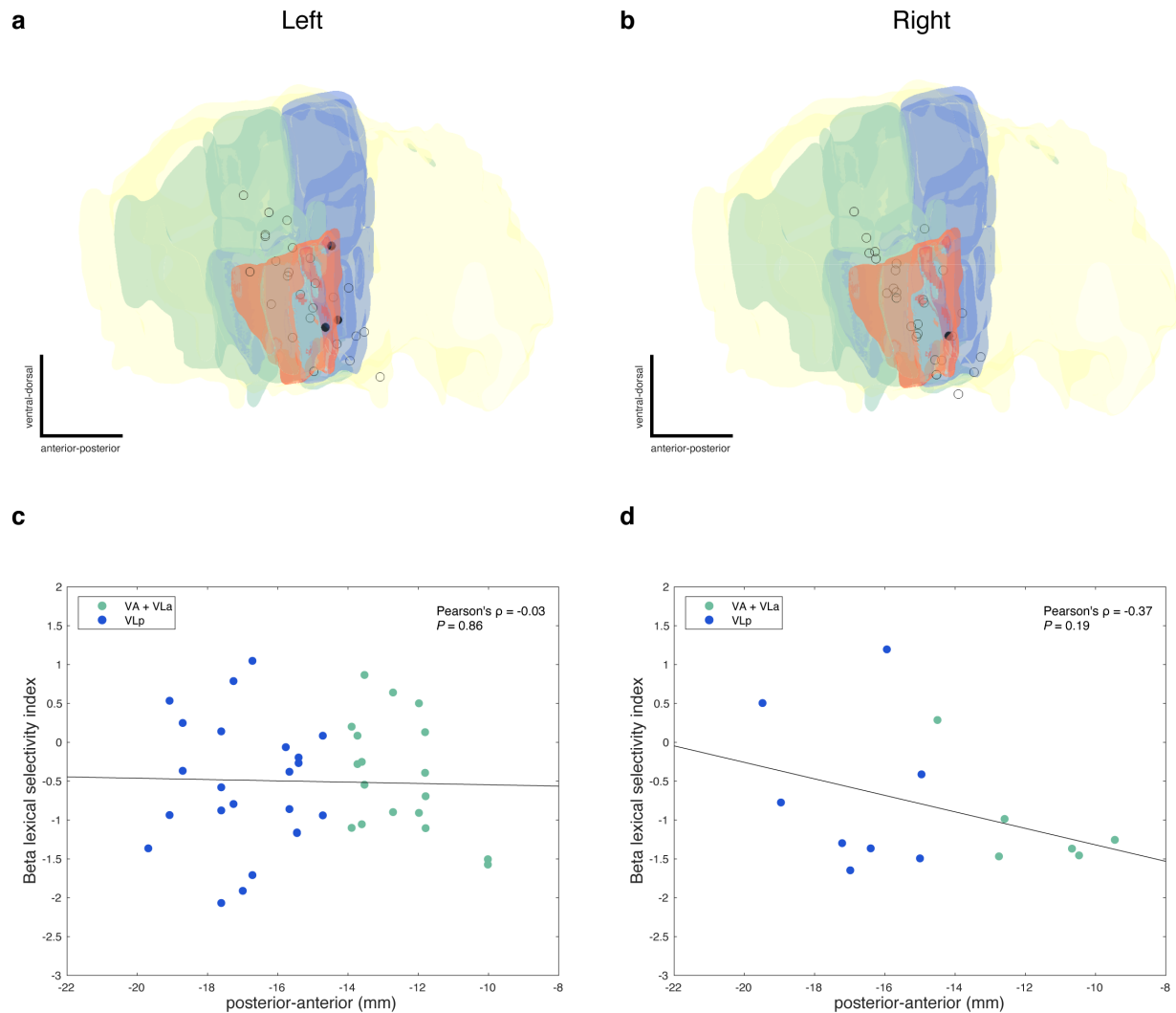
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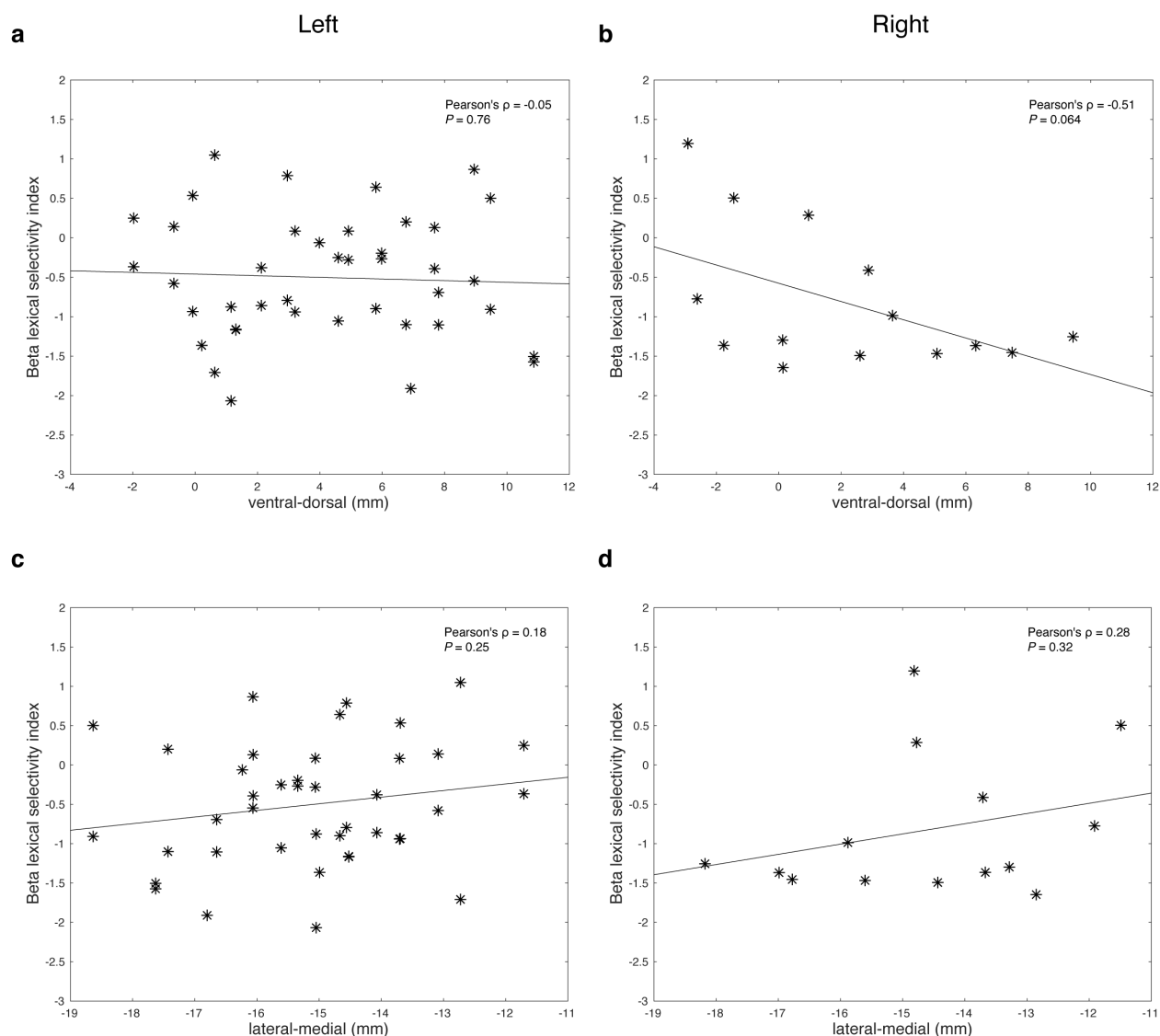
789 **Supplementary Figure 3: Correlation between right thalamic broadband gamma lexical**
790 **selectivity and recording locations along ventral-dorsal and lateral-medial axes.**

791 Broadband gamma lexical selectivity indexes of right side lead recordings that showed
792 significant task-related broadband gamma increase responses are correlated (Pearson's
793 correlation, $\alpha=0.05$) with ventral-dorsal locations (**a**) and lateral-medial locations (**b**) of the
794 recordings, respectively.



795

796 **Supplementary Figure 4: Beta lexical selectivity does not depend on anterior-posterior**
797 **location of the recording in either side. a** Left side lead recording sites are plotted together
798 with anatomical structures (thalamus in yellow, VA and VLa in green, VLp in blue, and Vim in
799 orange), viewed from a lateral direction. Recording sites where significantly nonword-selective
800 recordings in terms of beta response amplitudes (beta lexical selectivity index < -1.645 based on
801 normal approximation of t-distribution) were observed in either session are filled with black, and
802 remaining recording sites are shown in open circles. **b** Right side lead recording sites are flipped
803 to the left and plotted in the same way. **c** Beta lexical selectivity indexes of left side lead
804 recordings that showed significant task-related beta decrease responses are correlated
805 (Pearson's correlation, $\alpha=0.05$) with recording locations along the anterior-posterior axis. **d** Beta
806 lexical selectivity indexes of right side lead recordings that showed significant task-related beta
807 decrease responses are correlated (Pearson's correlation, $\alpha=0.05$) with recording locations
808 along the anterior-posterior axis. In **c** and **d**, recordings inside VA or VLa are green-colored and
809 recordings inside VLp are blue-colored.



810

811 **Supplementary Figure 5: Correlation between thalamic beta lexical selectivity and**
812 **recording locations along ventral-dorsal and lateral-medial axes. a, c** Beta lexical
813 selectivity indexes of left side lead recordings that showed significant task-related beta decrease
814 responses are correlated (Pearson's correlation, $\alpha=0.05$) with ventral-dorsal locations (a) and
815 lateral-medial locations (c) of the recordings, respectively. **b, d** Beta lexical selectivity indexes of
816 right side lead recordings that showed significant task-related beta decrease responses are
817 correlated (Pearson's correlation, $\alpha=0.05$) with ventral-dorsal locations (b) and lateral-medial
818 locations (d) of the recordings, respectively.

819 **Supplementary Table 1: Broadband gamma increase response and beta decrease**
 820 **response differ in locking properties.**

| Response type | Number of recordings | Stimulus-locked (%) | Speech-locked (%) | Not locked (%) |
|-----------------------------------|----------------------|---------------------|-------------------|----------------|
| Broadband gamma increase response | 91 | 19 (21) | 70 (77) | 2 (2) |
| Beta decrease response | 66 | 43 (65) | 19 (29) | 4 (6) |
| χ^2 | - | 31.4 | 36.1 | 1.55 |
| <i>P</i> | - | $< 10^{-5}$ | $< 10^{-5}$ | 0.21 |

821
 822 **Supplementary Table 2: Locking properties of broadband gamma increase response and**
 823 **beta decrease response do not differ between recording sides.**

| Response type | Number of recordings | Stimulus-locked (%) | Speech-locked (%) | Not locked (%) |
|-----------------------------------|----------------------|---------------------|-------------------|----------------|
| Broadband gamma increase response | | | | |
| Left | 59 | 10 (17) | 47 (80) | 2 (3) |
| Right | 32 | 9 (28) | 23 (72) | 0 (0) |
| χ^2 | 2.49 | | | |
| <i>P</i> | 0.29 | | | |
| Beta decrease response | | | | |
| Left | 49 | 31 (63) | 14 (29) | 4 (8) |
| Right | 17 | 12 (71) | 5 (29) | 0 (0) |
| χ^2 | 1.50 | | | |
| <i>P</i> | 0.47 | | | |

824

825 **Supplementary Table 3: Stimulus lists.**

| Stimulus list 1 | | Stimulus list 2 | | Stimulus list 3 | | Stimulus list 4 | |
|-----------------|---------|-----------------|---------|-----------------|---------|-----------------|---------|
| First 60 | Last 60 | First 60 | Last 60 | First 60 | Last 60 | First 60 | Last 60 |
| daif | daif | dight | dight | deave | deave | dipe | dipe |
| van | dutt | void | dute | vowed | doif | vote | doan |
| dutt | foat | dute | fape | doif | feam | doan | fode |
| vied | fute | vet | foon | vat | feeve | vain | fett |
| foat | meef | fape | mide | feam | vune | fode | meave |
| town | mipe | type | tep | tied | mafe | towed | mep |
| fute | neave | foon | veem | feeve | mupe | fett | neam |
| teed | nime | tune | naid | team | nipe | time | noit |
| meef | paim | mide | noop | vune | noove | meave | peff |
| putt | pote | pain | pime | poof | pode | pine | poom |
| mipe | teeve | tep | peaf | mafe | poun | mep | taid |
| pout | toff | peeve | taff | pave | teep | phone | tife |
| neave | vapp | veem | toove | mupe | tem | neam | vadd |
| note | vife | node | vade | need | vight | paid | vate |
| nime | vean | naid | vome | nipe | ved | noit | veet |
| moon | laz | mood | zool | moat | soith | neat | leeth |
| paim | saith | noop | loath | noove | luth | peff | sish |
| mauve | lesh | mean | luss | main | losh | mode | luthe |
| pote | rel | pime | rall | pode | rith | poom | ral |
| knife | reez | knot | suzz | knight | ruzz | might | riz |
| teeve | shuss | peaf | saze | poun | sar | taid | soush |
| fought | shule | fight | seash | foot | shoss | knit | shar |
| toff | sosh | taff | shez | teep | shiz | tife | shoth |
| five | sithe | feed | shile | foam | sile | food | thaze |
| vapp | thace | toove | thar | tem | thale | vadd | theal |
| fade | thauz | fame | thil | fain | thall | fate | sule |
| vife | thole | vade | thure | vight | thice | vate | sazz |
| deep | thoss | dine | thush | doubt | thel | dive | thosh |
| vean | zal | vome | zel | ved | zoice | veet | zoil |
| dawn | zole | date | soth | dime | zus | dean | zil |
| laz | daif | zool | dight | soith | deave | leeth | dipe |

| | | | | | | | |
|---------|-------|-------|-------|-------|-------|-------|-------|
| zoom | dutt | zone | dute | zip | doif | zap | doan |
| saith | foat | loath | fape | luth | feam | sish | fode |
| thought | fute | thud | foon | thumb | feeve | thief | fett |
| lesh | meef | luss | mide | losh | vune | luthe | meave |
| thin | mipe | theme | tep | that | mafe | them | mep |
| rel | neave | rall | veem | rith | mupe | ral | neam |
| this | nime | wrath | naid | zeal | nipe | thus | noit |
| reez | paim | suzz | noop | ruzz | noove | riz | peff |
| shoes | pote | these | pime | those | pode | thaws | poom |
| shuss | teeve | saze | peaf | sar | poun | soush | taid |
| shawl | toff | sure | taff | south | teep | shies | tife |
| shule | vapp | seash | toove | shoss | tem | shar | vadd |
| sell | vife | soar | vade | sill | vight | sews | vate |
| sosh | vean | shez | vome | shiz | ved | shoth | veet |
| sear | laz | size | zool | shore | soith | sale | leeth |
| sithe | saith | shile | loath | sile | luth | thaze | sish |
| sash | lesh | shell | luss | shale | losh | share | luthe |
| thace | rel | thar | rall | thale | rith | theal | ral |
| rush | reez | seal | suzz | role | ruzz | lace | riz |
| thauz | shuss | thil | saze | thall | sar | sule | soush |
| rise | shule | rose | seash | rash | shoss | lash | shar |
| thole | sosh | thure | shez | thice | shiz | sazz | shoth |
| race | sithe | rail | shile | raise | sile | lore | thaze |
| thoss | thace | thush | thar | thel | thale | thosh | theal |
| loathe | thauz | loss | thil | lure | thall | lose | sule |
| zal | thole | zel | thure | zoice | thice | zoil | sazz |
| laze | thoss | lies | thush | lows | thel | rule | thosh |
| zole | zal | soth | zel | zus | zoice | zil | zoil |
| laws | zole | leash | soth | lice | zus | rice | zil |

826

827

828 **Supplementary Table 4: *P* values of statistical tests comparing psycholinguistic**
829 **parameters between word and nonword stimuli.**

| | Stimulus list 1 | Stimulus list 2 | Stimulus list 3 | Stimulus list 4 |
|--|-----------------|-----------------|-----------------|-----------------|
| Weighted phonological neighborhood density | 0.23 | 0.43 | 0.88 | 0.86 |
| Summed bigram frequency | 0.97 | 0.51 | 0.39 | 0.32 |
| Summed phoneme probability | 0.47 | 0.33 | 0.37 | 0.51 |
| Summed biphone probability | 0.65 | 0.65 | 0.65 | 0.90 |

830 Two-tailed two-sample t-test, n=60, $\alpha=0.05$.