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Simultaneously recorded subthalamic and cortical LFPs reveal different lexicality effects during reading aloud

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ABSTRACT

Many language functions are traditionally assigned to cortical brain areas, leaving the contributions of subcortical structures to language processing largely unspecified. The present study examines a potential role of the subthalamic nucleus (STN) in lexical processing, specifically, reading aloud of words (e.g., ‘fate’) and pseudowords (e.g., ‘fape’). We recorded local field potentials simultaneously from the STN and the cortex (precentral, postcentral, and superior temporal gyri) of 13 people with Parkinson’s disease undergoing awake deep brain stimulation and compared STN’s lexically-related neural activity with that of the cortex. Both STN and cortical activity demonstrated significant task-related modulations, but the lexically effects were different in the two brain structures. In the STN, an increase in gamma band activity (31–70 Hz) was present in pseudoword trials compared to word trials during subjects’ spoken response. In the cortex, a greater decrease in beta band activity (12–30 Hz) was observed for pseudowords in the precentral gyrus. Additionally, 11 individual cortical sites showed lexically effects with varying temporal and topographic characteristics in the alpha and beta frequency bands. These findings suggest that the STN and the sampled cortical regions are involved differently in the processing of lexical distinctions.

1. Introduction

Although language function is classically considered to be supported by perisylvian cortical regions, accumulated clinical and electrophysiological evidence of the basal ganglia’s involvement in various language functions has led scientists to propose that these

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nuclei may constitute an important node in the language network, emphasizing their role in initiation, planning, monitoring, selection and coordination processes (e.g., Bohland, Bullock, & Guenther, 2010; Crosson, Zawacki, Brinson, Lu, & Sadek, 1997; Eisinger, Urdaneta, Foote, Okun, & Gunduz, 2018; Guenther, Ghosh, & Tourville, 2006; Indefrey, 2011; Jürgens, 2002; Kotz & Schwartz, 2010; Kotz, Schwartz, & Schmidt-Kassow, 2009; Middleton & Strick, 1994; Price, 2012; Tourville & Guenther, 2011; Ullman, 2004). Despite this progress, the precise contributions of the basal ganglia to language processing remain underspecified because non-invasive electrophysiological methods do not provide high enough resolution for measuring subcortical activity, especially of small-volume structures like the subthalamic nucleus (STN). The present study examines lexicality effects on local field potentials (LFPs) recorded intracranially from the STN while individuals with Parkinson's disease undergo functional neurosurgery for deep brain stimulation (DBS). To allow for cortical-subcortical comparisons, STN LFPs are recorded simultaneously with the electrocorticographic (ECoG) signal from a subset of cortical regions (precentral, postcentral, and superior temporal gyri) of the same patients while they read aloud real English words and phonotactically legal pseudowords.

Real words are believed to have fully specified lexico-phonological, semantic and morphosyntactic representations in the speaker's mind, while novel words encountered for the first time, such as pseudowords, lack these properties. Due to these differences, the processing of real words and pseudowords may recruit different mechanisms (Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001, 1993; Maris & de Graaff Stoffers, 2009; Zorzi, Houghton, & Butterworth, 1998) and different brain regions. In the cortex, increased activity for words as compared to pseudowords in left (or sometimes bilateral) middle and inferior temporal regions and regions around the left temporo-parietal junction is often taken to reflect the operations of lexico-semantic processes (Kotz, Cappa, von Cramon, & Friederici, 2002; Raettig & Kotz, 2008; Rissman, Eliassen, & Blumstein, 2003; Taylor, Rastle, & Davis, 2013; Vigneau, Jobard, Mazoyer, & Tzourio-Mazoyer, 2005). Heightened activity for pseudowords as compared to words in the left fusiform gyrus (Fiez, Balota, Raichle, & Petersen, 1999; Taylor et al., 2013; Woolnough et al., 2021) and the left frontal areas, primarily the inferior frontal gyrus (Dietz, Jones, Gareau, Zeffiro, & Eden, 2005; Fiebach, Friederici, Müller, & Cramon, 2002; Fiez et al., 1999; Hagoort et al., 1999; Heim et al., 2005, 2013; Xiao et al., 2005), is interpreted as evidence of greater reliance on grapheme-to-phoneme conversion processes and/or lexical costs (due to a more effortful search in the mental lexicon for a lexical entry that does not exist).

The present study examines whether differences in the processing of words versus pseudowords can also be observed in the subthalamic nucleus of the basal ganglia. The STN is considered to be a major regulator of motor function and a critical relay station between various cortical and subcortical regions due to its widespread anatomical connections within the looped architecture of the cortico-striatal-thalamic network (Alexander, DeLong, & Strick, 1986; Haynes & Haber, 2013; Simonyan, 2019; Temel, Blokland, Steinbusch, & Visser-Vandewalle, 2005; Volkmann, Daniels, & Witt, 2010). The STN's role within the network has been extended to suggest its involvement in higher-order cognitive functions (Eisinger et al., 2018; Kotz et al., 2009; Middleton & Strick, 1994), including speech and language. Clinically, this is evidenced by deficits in speech (hypokinetic dysarthria, articulatory imprecision, diminished prosody) in patients with degenerative disorders of the basal ganglia, e.g., Parkinson's disease (Aldridge, Theodoros, Angwin, & Vogel, 2016), and impairment of phonemic and semantic verbal fluency as a frequent sequela of STN-DBS (for a review, see Parsons, Rogers, Braaten, Woods, and Tröster (2006)). Electrophysiological data also suggest that the STN is involved in speech and language-related processes (Chrabaszcz et al., 2019; Hebb, Darvas, & Miller, 2012; Lipski et al., 2018; Watson & Montgomery, 2006; Wojtecki, Elben, Vesper, & Schnitzler, 2017).

Especially relevant for the current study is work that implicates the STN and other basal ganglia nuclei in aspects of lexico-semantic processing. For example, Anzak and colleagues found that STN broad gamma (30–95 Hz) power increased and beta (13–30 Hz) power decreased during phonemic and semantic verbal fluency tasks, after controlling for motor components of verbal response generation (Anzak et al., 2011). Hohlefeld and colleagues administered a lexical decision task to Parkinson's patients undergoing STN-DBS and found a significant positive correlation between cortico-subthalamic neural coherence and patients' response accuracy in the beta frequency range (14–35 Hz), suggesting the relevance of cortico-subthalamic interactions for lexical decisions (Hohlefeld et al., 2017). Finally, lexico-semantic neural responses have been observed in other nuclei of the basal ganglia (e.g., Abdullaev & Melnichuk, 1997; Crosson et al., 2003) and the thalamus (e.g., Tiedt et al., 2017; Wahl et al., 2008; Wang et al., 2020; for a review, see Llano, 2013), using different methods and experimental paradigms. Given that the STN has strong connections with these subcortical structures via multiple afferent and efferent pathways (Hamani, Saint-Cyr, Fraser, Kaplitt, & Lozano, 2004), it is likely that the STN is also involved in some aspects of lexical processing.

The current study extends this past work in two important respects. It is the first study to contrast cortical (precentral, postcentral, and superior temporal gyri) and STN neuronal activity during processing of two types of theoretically distinguished linguistic stimuli (words versus pseudowords). Previous studies examining modulation of regional electrical activity in the cortex in response to the two types of stimuli have shown that pseudowords elicit more power in the gamma (30–70 Hz) and high gamma (70–150 Hz) frequency ranges compared to real words (Cibelli, Leonard, Johnson, & Chang, 2015; Juphard et al., 2011; Mainy et al., 2008; Tanji, Suzuki, Delorme, Shamoto, & Nakasato, 2005; Woolnough et al., 2021). The fact that such gamma modulations were localized to the cortical regions commonly implicated in orthographo-phonological processes suggests that low-level sublexical information may bind together for word recognition by means of gamma oscillations. In the STN, gamma power modulations have also been observed, either as an induced response in the spectra of LFP activity at rest (e.g., Brown et al., 2001), or as a response to voluntary movement (e.g., Androulidakis et al., 2007) and speech (Chrabaszcz et al., 2019). It has been shown to scale with kinematic parameters and correlate negatively with motor symptom severity in Parkinson's patients (Lofredi et al., 2018), pointing at its prokinetic nature. However, no study has yet reported whether STN activity in the gamma frequency band or in any other canonically defined EEG band is modulated by lexical distinctions.

Second, it is the first study to compare STN and cortical activity for words versus pseudowords with a reading aloud task, which allows for lexical effects associated with written stimulus presentation versus speech production to be separately probed. In skilled

Table 1
Demographic and clinical characteristics of patients (UPDRS = Unified Parkinson's Disease Rating Scale).

Subject	Gender	Age	Handedness	Education, years	Duration of disease, years	Predominant symptoms of PD	Hoehn and Yahr Stage	UPDRS Score (off medication)	UPDRS Score (on medication)	Number of cortical recording sites	Number of STN recording sites
1	M	71	NA	NA	6	Activation tremor; resting tremor; bradykinesia; rigidity	2	35	22	5	6
2	M	60	R	12	14	Resting tremor; Rigidity	2	53	47	16	Not recorded
3	F	52	L	12	18.6	Bradykinesia; gait difficulties; freezing	2	26	18	15	4
4	M	68	R	14	9	Bradykinesia; gait difficulties; resting tremor; rigidity	2	46	31	4	12
5	M	60	R	16	5	Resting tremor; rigidity	2	31	17	Excluded	6
6	M	68	L	16	8	Resting tremor	2	50	33	28	6
7	M	57	NA	16	7	Gait difficulties; resting tremor	2	44	10	4	6
8	M	82	R	16	8	Bradykinesia; rigidity	2	36	21	6	9
9	M	66	R	19	7	Resting tremor	2	45	28	17	12
10	M	66	R	20	14.2	Gait difficulties; rigidity	3	44	27	24	6
11	F	71	R	16	8	Activation tremor; resting tremor	2	24	13	4	9
12	M	77	R	18	10	Activation tremor; bradykinesia; resting tremor	2	27	17	Excluded	4
13	M	59	R	13	6	Activation tremor; bradykinesia; rigidity	2	39	25	34	12

Note. Number of cortical and STN recording sites reflects only those sites that were included in the analysis. M = male, F = female, R = right, L = left.

readers, such as the participants in this study, the processes that give rise to phonological access and word recognition are triggered automatically by the onset of orthographic stimuli and occur within the first 400–500 ms following stimulus onset (Indefrey, 2011; Indefrey & Levelt, 2004). Most theoretical models of reading presuppose that different processes (lexical versus sublexical) dominate this initial stage of reading depending on the lexical status of the stimuli — words or pseudowords, respectively. If these processes involve the STN and the sampled cortical regions directly or indirectly, their involvement should manifest within the first 500 ms of the reading aloud task. Alternatively, if their involvement in reading aloud is driven by motor aspects of speech, such as the differences in the production of familiar versus unfamiliar syllables and phonetic sequences, differences in the neuronal activity for words versus pseudowords should be observed during spoken responses.

2. Methods

2.1. Participants

Data were collected from 13 native English-speaking patients with Parkinson's disease (11 M/2F; age: 65.9 ± 8.3 years; duration of disease: 9.3 ± 4 years; duration of education: 15.7 ± 2.6 years) undergoing awake stereotactic neurosurgery for bilateral implantation of DBS electrodes in the STN. All patients except one were classified to be at stage 2 of disease progression according to the Hoehn and Yahr scale (Hoehn & Yahr, 1967) and scored 38.5 ± 9.5 on the Unified Parkinson's Disease Rating Scale (UPDRS). Subjects' demographic and clinical characteristics are provided in Table 1. In addition to the clinically indicated implantation of depth electrodes, participants were temporarily implanted with subdural ECoG arrays over the left lateral cortex. Dopaminergic medication was withdrawn the night before surgery. All procedures were approved by the University of Pittsburgh Institutional Review Board (IRB Protocol # PRO13110420), and all patients provided informed consent to participate in the study.

2.2. Stimuli

A total of 240 stimuli (120 words and 120 word-like phonotactically legal but meaningless pseudowords) were constructed. Each of the stimuli consisted of one consonant-vowel-consonant (CVC) syllable, e.g., 'fame' vs. 'fape'. Pseudowords were constructed by changing either the vowel or the final consonant of existing words. Phonemes in words and pseudowords were balanced to control for possible articulatory differences between the two types of stimuli; no phoneme was repeated within a CVC syllable. Additionally, the stimuli were balanced along a number of psycholinguistic parameters shown to affect reading performance, such as number of letters, phonological neighborhood density, bigram frequency, etc. (See Table 2 for stimuli characteristics together with the outcomes of statistical comparisons between the two conditions). These psycholinguistic measures were computed using the English Lexicon Project database (Balota et al., 2007). For a detailed description of how the stimuli were constructed and balanced, see Moore, Fiez, and Tompkins (2017). Words and pseudowords were split into 4 presentation lists with 60 trials each (30 unique words and 30 unique pseudowords). Presentation of words and pseudowords within these 60 trials was alternated.

2.3. Procedure

The stimuli were created and presented in Psychophysics Toolbox extensions (Brainard, 1997) running on the MATLAB platform (MathWorks, Natick, MA). A schematic of the experimental procedure is shown in Fig. 1. First, participants were presented with a white fixation cross against the black screen (intertrial interval, ITI), after which a green fixation cross (preparatory cue) appeared on the screen, prompting participants to get ready for a response. After that the screen remained black for a short period of time (interstimulus interval, ISI) before a word (e.g., 'fame') or a pseudoword (e.g., 'fape') appeared on the screen and participants were instructed to read it out loud. The stimulus remained on the screen until participants made the response, after which the experimenter advanced the presentation to the next trial. On certain trials, task presentation was paused by the experimenter at varying times during the trial to provide feedback to the participants about their performance (e.g., to speak louder), address their requests (e.g., adjust the position), inquire about their state (e.g., fatigue), etc. This resulted in variable values for the ITI period (mean = 1000 ms, SD = 850 ms), preparatory cue (mean = 350 ms, SD = 560 ms), and ISI period (mean = 700 ms, SD = 220 ms). Participants performed the reading aloud task during the subcortical mapping portion of the surgery, at up to four different recording locations within the STN. A different stimulus list was presented to participants during each recording session. Participants were familiarized with the task prior to surgery.

Table 2
Stimuli characteristics.

Parameter	Words		Pseudowords		t value	p value
	Mean	SD	Mean	SD		
Word frequency (log-transformed) (taken from HAL database)	9.09	2.46	–	–	–	–
Length (in letters)	4.25	0.61	4.17	0.62	–0.95	0.35
Phonological neighborhood (weighted)	2807.66	3724.72	3121.20	7265.17	0.42	0.67
Bigram frequency (summed)	1833.36	692.48	1721.51	648.89	–1.29	0.20
Phoneme probability (summed)	0.13	0.04	0.13	0.04	–1.63	0.10

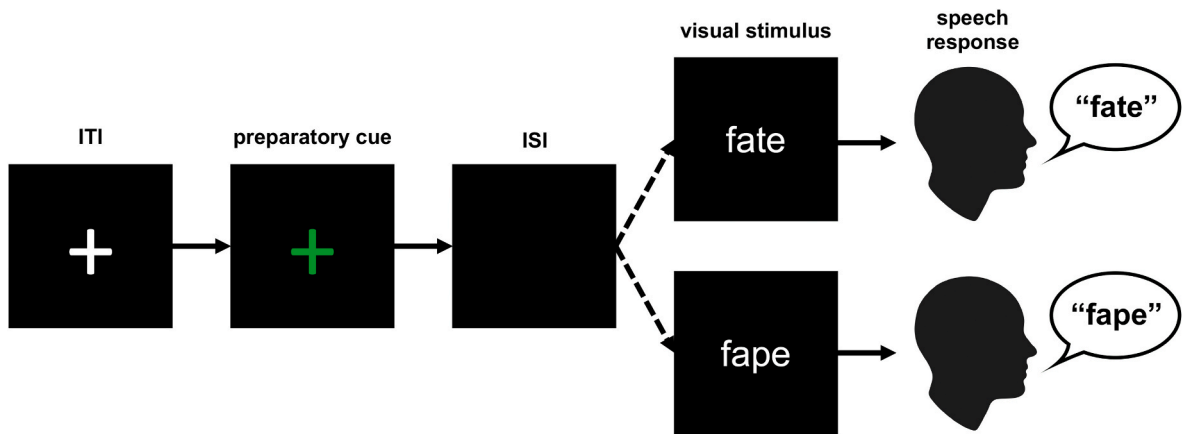


Fig. 1. Experimental paradigm. ITI = intertrial interval; ISI = interstimulus interval.

2.4. Audio recordings

Participants' responses were recorded using an omnidirectional microphone (Audio-Technica ATR3350iS Mic, frequency response 50–18,000 Hz, or PreSonus PRM1 Mic, frequency response 20–20,000 Hz). The microphone was positioned at approximately 8 cm and 45° from the subjects' left mouth angle. The audio signal was recorded using a Zoom H6 digital recorder (sampling rate 96 kHz). One line out of the Zoom H6 recorder was connected as an analog input to the Grapevine Neural Interface Processor (Ripple LLC, Salt Lake City, UT, USA), which recorded the audio signal at the sampling rate of 30 kHz. This channel was used for offline synchronization between the high-fidelity 96 kHz audio recordings and the ECoG recordings, ensuring sub-millisecond synchronization precision. The audio and the ECoG recordings were then synchronized with the neural recordings from the STN using digital pulses delivered to the Neuro-Omega system (Alpha Omega, Nazareth, Israel) via a USB data acquisition unit (Measurement Computing, Norton, MA, model USB-1208FS). The digitized audio recordings were segmented and transcribed offline by trained communication science students in a custom-designed graphical user interface (GUI) implemented in MATLAB environment. Twenty percent of all transcribed data was checked by a senior student for reliability purposes. Trials were included in the analysis if subjects' spoken responses were unambiguously identified by the raters. All responses were scored to indicate whether subjects produced the intended words and pseudowords. For each trial, the onsets and offsets of the visual stimulus and the spoken response were marked.

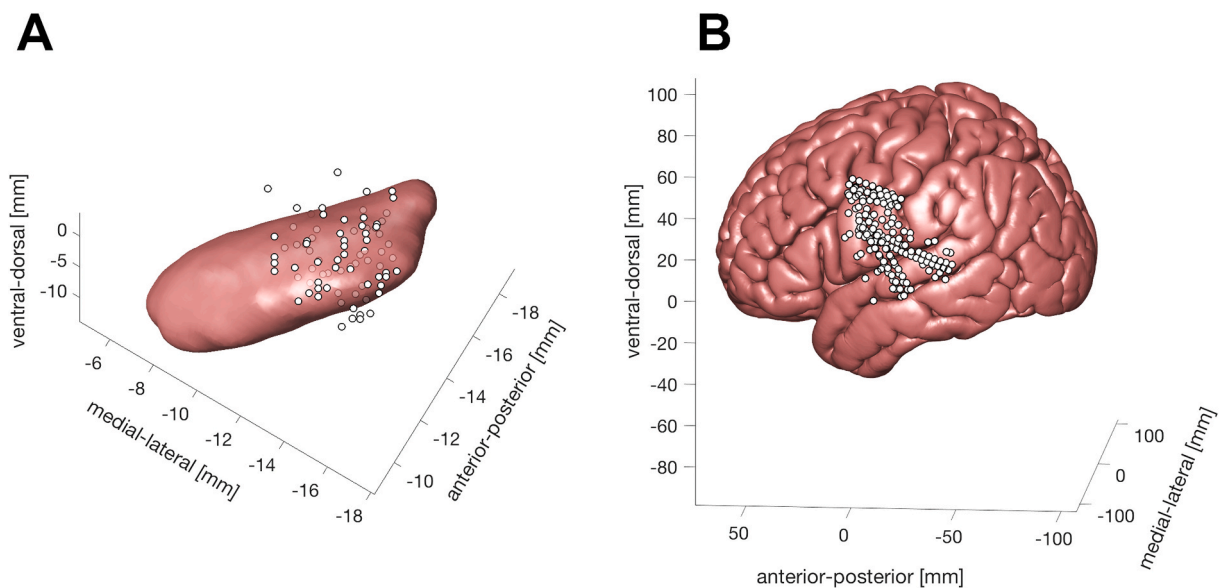


Fig. 2. STN and cortical recording sites. MNI-defined reconstructed locations of recording sites in A) the STN (n = 92) and B) cortex (n = 157) that were included in the analysis.

2.5. Subthalamic nucleus recordings

Subjects were implanted with DBS electrodes bilaterally, but the reading aloud task was administered only during the electrophysiological mapping of the left-side STN (always the first side to be implanted according to the surgical routine). Accordingly, LFPs were recorded only from the left STN. LFPs were recorded from the mapping electrode's stainless-steel macroelectrode ring (0.55 mm in diameter, 1.4 mm in length), which is located 3 mm above the parylene insulated tungsten microelectrode tip (25 μ m in diameter, 100 μ m in length). Two or three mapping electrodes were used per subject. They were oriented on the microtargeting drive system using a standard cross-shaped Ben-Gun array with a 2 mm center-to-center spacing and targeted the dorsolateral area of the STN, as described by Lee et al. (2018). The mapping electrodes were advanced manually in 0.1 mm steps starting 15 mm above the defined target. Once the surgeon and the neurophysiologist determined that the electrode had entered the STN based on the neuronal discharge characteristic of single-unit neuronal activity, the reading task was administered up to 4 times as the electrodes advanced more inferiorly through the STN. Accordingly, LFP recordings could be obtained from up to 4 different depths of the STN per subject. Data from one subject (see Table 1, subject #2) were not recorded due to a technical problem. As a result, STN LFP data were collected from a total of 92 recording sites across 12 patients. The LFP signal was recorded with the Neuro-Omega data acquisition system at a sampling rate of 44 kHz and was band-pass filtered at 0.075 Hz to 10 kHz. The LFP signal was referenced online to the guide cannula that was inserted in the brain to carry microelectrodes. The coordinates of the STN recording sites were determined using a semi-automatic approach implemented in the Lead-DBS toolbox (Horn & Kühn, 2015). Post-operative CT scans were coregistered with pre-operative MRI scans using open-source Advanced Normalization Tools (ANTs) and normalized to MNI ICBM152 NLIN 2009b stereotactic space. MNI-defined coordinates of recording sites were then extracted and visualized on the DISTAL atlas by Ewert et al. (2018) in Fig. 2A.

2.6. Cortical recordings

In addition to the clinically indicated implantation of subcortical electrodes, all patients were temporarily implanted with ECoG electrode arrays over the left lateral cortical surface of the brain. They were inserted through the cranial burr hole made for the insertion of STN guide tubes. The ECoG signal was acquired at 30 kHz using the Grapevine Neural Interface Processor. A needle electrode placed in the midline scalp (in the sterile field between the two burr holes) was used as the reference, and sterile needle placed in the shoulder was used as the ground. Most of the remaining subjects were implanted with 6- or 28-channel Ad-Tech electrode strips (Ad-Tech Medical Corporation, Racine, WI, USA) except for one subject who was implanted with a 36-channel PMT electrode strip (PMT Corporation, Chanhassen, MN, USA). Depending on the type of the strip, the electrode contacts varied in size (1, 2 or 4 mm in diameter) and center-to-center spacing (3, 4 or 10 mm). Two subjects were excluded from the analysis (see Table 1, subjects #5 and #12) due to an overly noisy signal across all recording channels. A total of 206 electrode contacts were placed over the left cortical surface, but only 157 were included in the analysis – those that were confined to the main regions of interest: precentral gyrus ($n = 48$), postcentral gyrus ($n = 60$), and superior temporal gyrus ($n = 49$) (see Fig. 2B for the locations of the electrodes that were included in the analysis). Other brain regions had very sparse electrode coverage; therefore, they were not included in the analysis. Electrodes were assigned to the regions of interest based on patients' individual brain morphology in the native brain space rather than the template brain in MNI (Montreal Neurological Institute) space. Localization of the electrodes on the cortical surface was performed according to the semi-automated procedure described in Randazzo et al. (2016) using intra-operative fluoroscopic images (512 \times 512 pixels, General Electric, OEC 9900), pre-operative computed tomography (CT) and magnetic resonance imaging (MRI) scans, and post-operative CT scans. Electrode locations were then registered to MNI ICBM152 brain space in Brainstorm (Tadel, Baillet, Mosher, Pantazis, & Leahy, 2011) (<https://neuroimage.usc.edu/brainstorm/>).

2.7. Electrophysiological data processing

Data processing was performed using custom code based on the FieldTrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011) in MATLAB (version 2017b). The LFP recordings were resampled at 1 kHz and band-pass filtered from 2 to 400 Hz. A notch filter at 60 Hz (and its harmonics) was applied to remove line noise. Next, the data were segmented into epochs starting 2 s before the presentation of the visual stimulus (a word or a pseudoword) on the screen and ending 2 s after subjects' response offset. The epoched data were visually inspected for noisy channels and artifactual trials, which were excluded from subsequent analyses. The remaining data were common-average referenced to minimize noise and artifactual electrode cross-talk. For spectrotemporal analysis, each trial's data were decomposed separately using Morlet wavelet transformation (width = 7 cycles) over frequencies of 2 Hz–200 Hz in increment steps of 2 Hz. Spectrotemporal decomposition, when applied to single trials, allows for the examination of task-induced versus task-evoked LFP power changes (Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1996; Tallon-Baudry & Bertrand, 1999). To account for any possible trial-level noise in the signal, each trial's time-frequency resolved power was normalized (z-scored) relative to the baseline, i.e., differenced from the baseline's mean power and divided by the baseline's standard deviation. Baseline was defined as a 1-s time interval preceding the presentation of the visual stimulus. Normalized time-frequency data were aligned either to the time of the stimulus presentation on the screen, to examine activity during stimulus encoding and reading, or to the time of the onset of the spoken response, to examine speech-related activity.

2.8. Data handling and statistical approach

All statistical analyses were performed in MATLAB 2017b and R version 3.4.4 (R Development Core Team, 2018). A within-subjects experimental design was used, in which all subjects received trials with both words and pseudowords. Time-frequency resolved power was computed on a trial-by-trial basis for each subject, recording session and recording site. The position of the ECoG electrode strips did not change from session to session, unlike the position of the STN electrodes (which progressed along the lead's implantation trajectory), therefore, cortical trial-level time-frequency data were combined across sessions per each cortical electrode. Because placement of electrodes varied across subjects and sometimes spanned different functional regions (e.g., sensorimotor, limbic and associative territories in the STN), data from all recording sites from all subjects were included in the analysis rather than taking the average across all recording sites per each subject. This resulted in 92 time x frequency x trial matrices corresponding to 92 distinct recording sites in the STN and 157 matrices of the same structure corresponding to 157 recording sites in the cortex. Cortical recording sites were further subdivided into three regions of interest (ROIs) based on their locations defined in the native brain space: precentral gyrus ($n = 48$), postcentral gyrus ($n = 60$), and superior temporal gyrus ($n = 49$). Hereon, cortical and STN data were analyzed using the same statistical approach.

To examine the lexicality effect in each of the brain regions, trials for each recording site were divided into two conditions (words and pseudowords) and averaged within the condition, resulting in matched word and pseudoword time-frequency power spectra for each of the recording sites in the STN and in the three cortical ROIs. This way, the statistical variance came from across recording sites. Cluster-based permutation tests (Maris & Oostenveld, 2007) were performed using a Matlab `permutest` function (Gerber, 2021) to evaluate i) at which times and frequencies power modulations within each of the two conditions (separately for the word and the pseudoword conditions) were significantly different from zero, and ii) at which times and frequencies power modulations were significantly different between the two conditions, i.e., words vs. pseudowords. We used a dependent-samples two-sided test with 1000 permutations; cluster p -values below 0.05 were considered significant.

Because this analysis included all electrodes across all subjects without accounting for the hierarchical structure of the data (namely, a different number of recording sites per each subject), in the next set of analyses we used a linear mixed-effects modeling approach (Baayen, Davidson, & Bates, 2008; Bagiella, Sloan, & Heitjan, 2000) to account for the problem of multiple observations per subject. First, time-frequency resolved power in the STN and the three cortical ROIs was averaged within five canonical EEG bands (theta 4–7 Hz, alpha 8–11 Hz, beta 12–30 Hz, gamma 31–70 Hz, and high gamma 71–150 Hz) for each recording site and two time windows corresponding to reading behavior (from stimulus onset until spoken response onset) and speaking behavior (from spoken response onset to its offset). Linear mixed-effects models included averaged power as a dependent variable, lexicality as a fixed factor, and subjects as a random factor, in order to control for the subject-related repeated measures and subject-level heterogeneity typically present in clinical populations. A separate LMEM was performed for each brain region ($n = 4$) and frequency band ($n = 5$), therefore family-wise error rate correction was applied, resulting in a Bonferroni corrected p value of 0.0025 ($0.05/(4*5) = 0.0025$). LMEMs were run using R package `lme4` (Bates, Maechler, Bolker, & Walker, 2015).

Finally, the third analysis aimed at identifying whether individual cortical or STN recording sites showed sensitivity to the lexicality manipulation, i.e., showed greater activity for one type of stimulus than the other. To this end, time-frequency resolved power in word and pseudoword trials was compared within each recording site. In this analysis, the statistical variance came from across trials. The same cluster-based permutation test as described above was used to evaluate differences between the two conditions with the exception that it was performed for independent samples due to the unmatched number of word and pseudoword trials per recording site as a result of the artifact rejection procedure. Recording sites with cluster p -values below 0.05 were considered responsive to the lexicality manipulation.

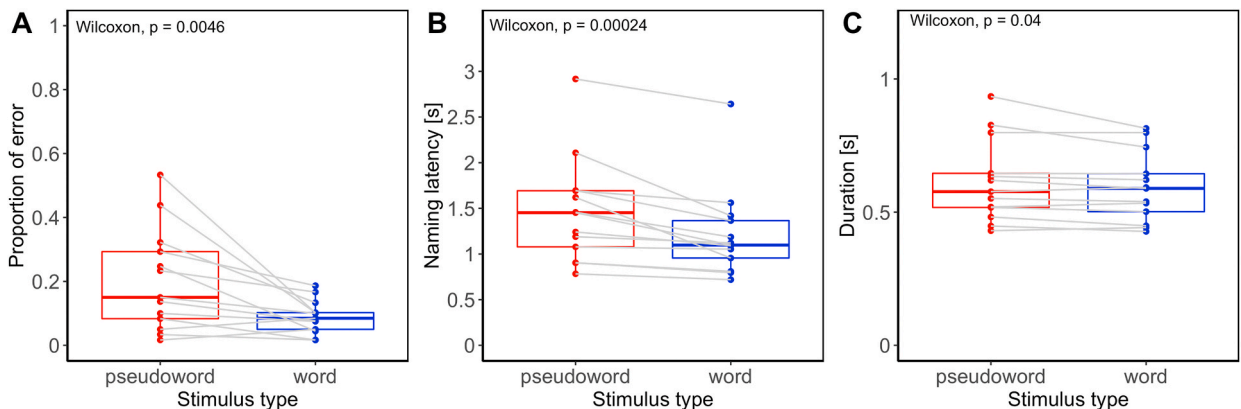


Fig. 3. Behavioral results. Differences between words and pseudowords in subjects' ($n = 13$) A) proportion of error, B) naming latency (in seconds), and C) response duration (in seconds).

3. Results

3.1. Behavioral results

Responses were scored as accurate if participants correctly produced a pseudoword in response to a stimulus pseudoword and a word in response to a stimulus word, otherwise they were scored as erroneous. The mean proportion of error was 0.14 (SD = 0.34); the mean duration of the spoken response was 0.59 s (SD = 0.21); the mean reading latency calculated from the presentation of the stimulus on the screen to the onset of the spoken response was 1.33 s (SD = 0.97). Behavioral measures did not correlate significantly with the severity of the disease symptoms as measured by the UPDRS either while the patients were off or on medication. Using a paired Wilcoxon signed rank test, we found significant differences in the subjects' proportion of error ($Z = 84, p = 0.0046$), response duration ($Z = 75, p = 0.04$) and reading latency ($Z = 91, p = 0.00024$) between word and pseudoword trials (Fig. 3). The former suggests that subjects experienced a lexical bias in that they tended to read out pseudowords as words (e.g., 'fape' instead of 'fate') significantly more frequently than words as pseudowords ('fape' instead of 'fate').

3.2. Electrophysiological results

3.2.1. Subthalamic nucleus

In the STN, a cluster-based permutation test including all recordings sites ($n = 92$) revealed statistically significant clusters of power modulations around the time of the patients' spoken responses in both the word and the pseudoword conditions (Fig. 4). Specifically, power decreases were observed in the lower frequency bands between 8 and 30 Hz (alpha, beta) and power increases were observed in higher frequency bands, above 30 Hz (gamma, high gamma). Power increases in the theta (4–8 Hz) frequency band were evident in the time window preceding subjects' response onsets in both types of trials. Subtracting power spectra of one condition from the other revealed an overall greater gamma power in the pseudoword trials compared to word trials, which did not appear to be aligned either to the stimulus presentation or the spoken response onset; rather, this effect spanned almost the entire duration of the trial from stimulus onset until response offset (Fig. 4). A significant cluster of increased gamma power in the pseudoword condition relative to the word condition was obtained within the speaking time window.

To account for possible influence of subject-level idiosyncrasies in the data, power in each of the above defined frequency bands was averaged for each subject and each recording site over the response duration window (response onset to response offset) and the stimulus window (stimulus presentation to response onset) and modeled using a linear mixed-effects approach. A significant lexicality effect with all recordings sites ($n = 92$) included in the model was observed only for the average power in the gamma frequency band during the response window ($\beta = 0.03, SE = 0.007, t = 3.85, p = 0.003$ after Bonferroni correction) (Fig. 5A), but not during the stimulus window ($\beta = 0.019, SE = 0.007, t = 2.87, p = 0.09$ after Bonferroni correction) after adjusting for family-wise error rate. Interestingly, while some recording sites demonstrated large effect sizes (Hedges' g) (Fig. 5B) and most subjects showed an overall greater gamma power in the pseudoword trials compared to word trials (Fig. 5C), gamma power differences between words and pseudowords at individual STN recording sites did not reach significance. Thus, the lexicality effect in the STN was only quantifiable at the group level.

Additionally, there was no particular topographic structure in the distribution of the observed differences between conditions over the subthalamic nucleus (Fig. 5B), when assessed with an LMEM, using Hedges' g as a dependent variable, the MNI-defined x, y, z coordinates as fixed factors, and subjects as random intercepts. Neither of the fixed factors significantly predicted the distribution of the differences between the two conditions in the gamma band power: $x: \beta = -0.1, SE = 0.08, t = -1.28, p = 0.2; y: \beta = -0.06, SE =$

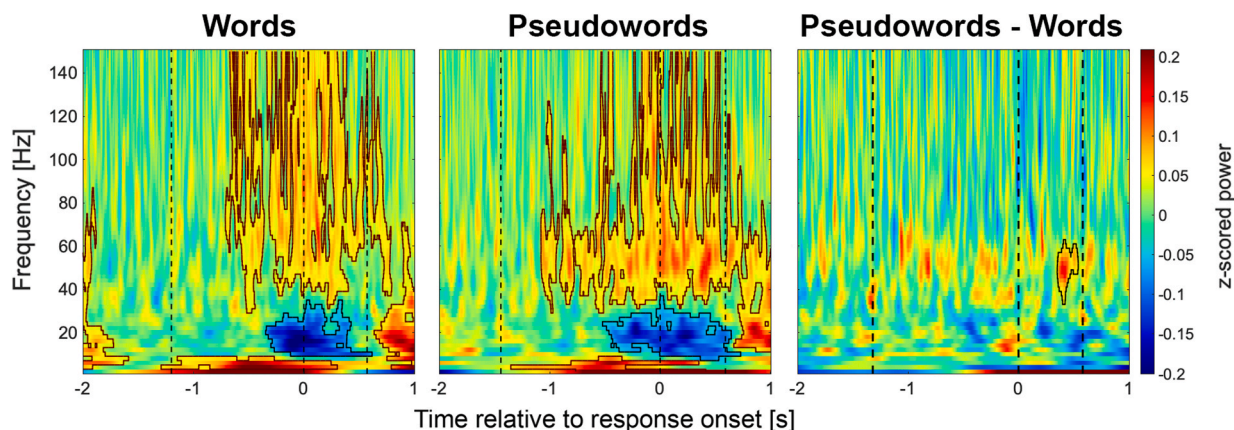


Fig. 4. Lexicality effects in the STN. Task-related power modulations in word and pseudoword trials averaged over all STN recording sites ($n = 92$) and the difference between the two conditions. Clusters with significant power modulations (cluster-based permutation tests, $p < 0.05$) are marked with brown (increases in power) or black (decreases in power) contour. Average times of stimulus presentation, response onset and response offset are marked with vertical black dashed lines (response onset = 0 s).

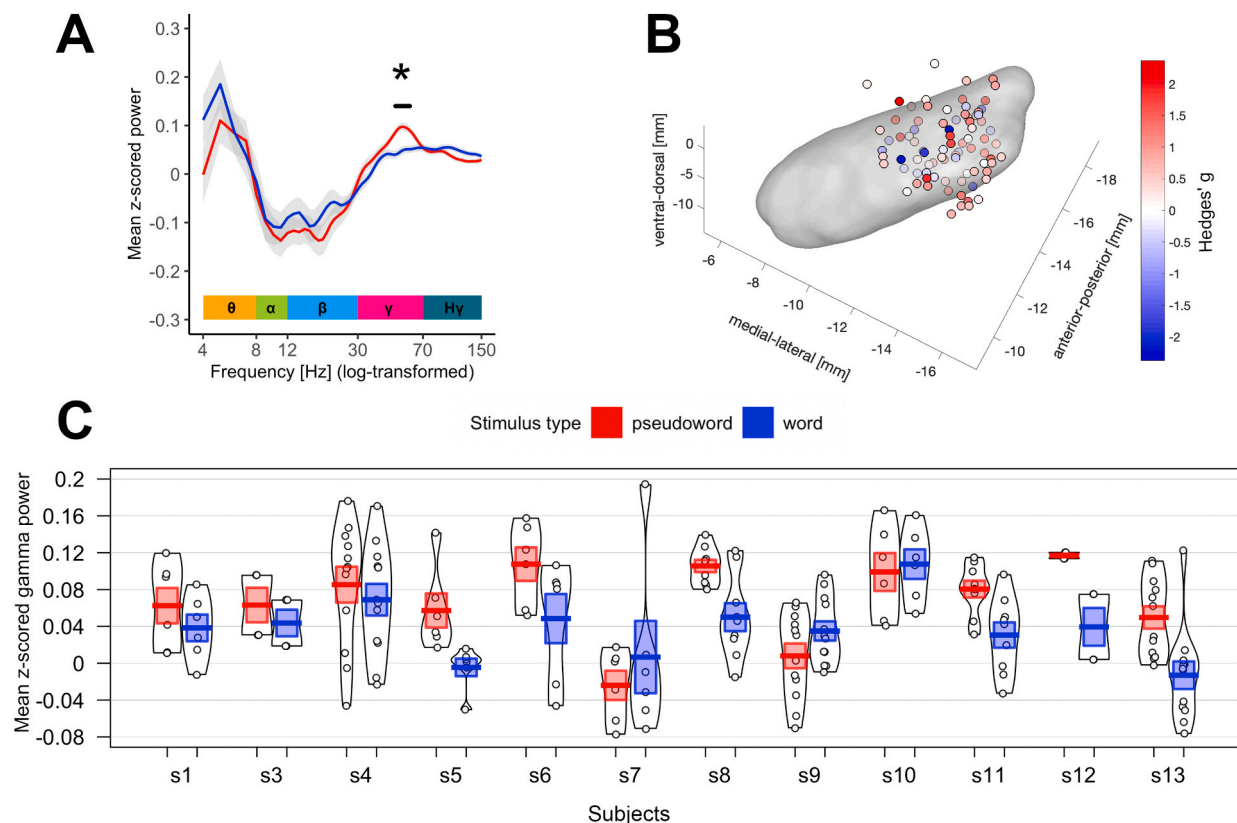


Fig. 5. Stimulus-induced gamma (31–70 Hz) power differences in the STN during subjects' spoken response. A) Z-scored spectral power during the spoken response window in the word trials (blue) vs. pseudoword trials (red) averaged over 92 recordings sites. The semi-transparent ribbon represents standard error of the mean. Asterisk marks the frequencies within the gamma range at which significant differences in the neural activity between word and pseudoword trials were observed based on the linear mixed-effects model with lexicality as a fixed factor and subjects as a random factor, $p < 0.05$, Bonferroni corrected. B) Distribution of lexicality effects (Hedges' g) over the STN recording sites. Each dot represents a recording site. C) Within-subject differences in the averaged z-scored gamma power between word and pseudoword trials. Dots represent STN recording sites. Beans represent smoothed density curve showing the full data distribution. Blue (words) and red (pseudowords) horizontal lines represent the mean; the correspondingly colored bands represent standard error of the mean.

0.08, $t = -0.83$, $p = 0.4$; $z: \beta = 0.02$, $SE = 0.05$, $t = 0.35$, $p = 0.7$. Subjects' observed behavior (error rate, response latency, and response duration) did not correlate significantly (Spearman's ρ , $p > 0.05$) with gamma activity during the response window, either when i) averaged across all types of trials, ii) averaged across word trials, iii) averaged across pseudoword trials, or iv) calculated as a difference between word and pseudoword conditions.

3.2.2. Cortex

Using cluster-based permutation tests with all cortical recording sites ($n = 157$) included in the analysis, we observed significant (cluster $p < 0.05$) task-related power modulations in the cortex during reading aloud of both words and pseudowords (Fig. 6). Power increases were observed in the higher frequency bands (above 50 Hz) in all of the three ROIs and were most prominent during the subjects' spoken responses. Power decreases in the lower frequency bands (below 50 Hz) were also observed in the three ROIs during the spoken response window, but the cluster with the decreased power in the STG was not significant in either the word or the pseudoword condition. In the precentral gyrus, power in the lower frequency bands started to decrease even earlier than in the postcentral gyrus and the STG. Subtracting power spectra of one condition from the other in each of the ROIs revealed stronger power decreases (cluster-based permutation tests, $p < 0.05$) in the pseudoword trials compared to word trials in the lower frequency ranges in the three brain structures. Additional clusters with significant power increases in the theta frequency range and the gamma/high gamma frequency range were observed in the postcentral gyrus (Fig. 6). Similar to the analysis of the STN data, power in each of the frequency bands was averaged per each recording site over the two time windows – stimulus window and response window – and modeled using the LMEM approach. The results revealed that differences between words and pseudowords were only significant in the precentral gyrus, with greater beta power decreases for pseudowords compared to words during the response production window ($\beta = 0.15$, $SE = 0.05$, $t = 3.24$, $p = 0.034$ after Bonferroni correction), but not the stimulus window ($\beta = 0.03$, $SE = 0.03$, $t = 1.2$, $p > 1$ after Bonferroni correction), after adjusting for family-wise error rate.

Next, we assessed whether individual cortical recording sites show differential power modulations to words vs. pseudowords. The

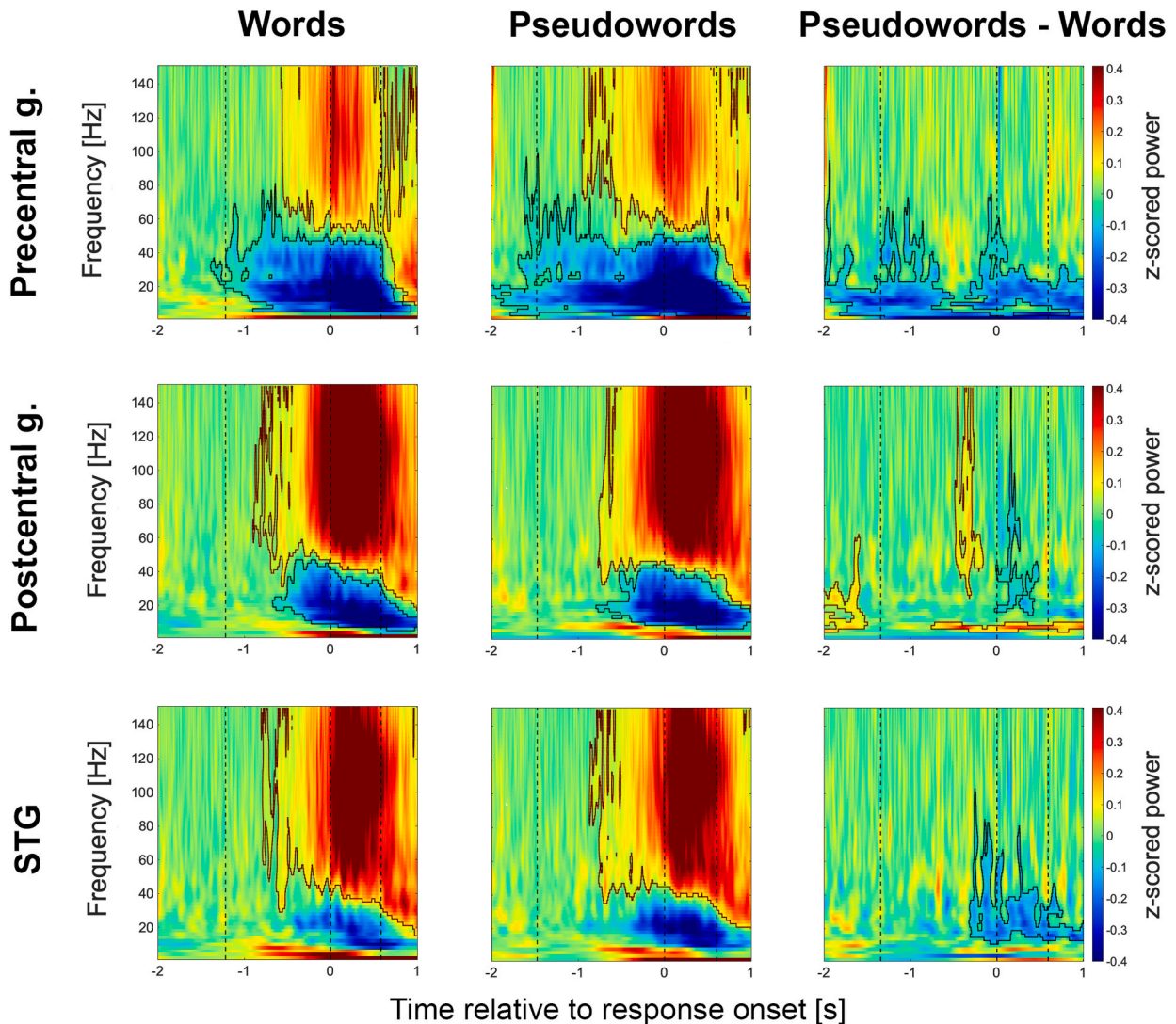


Fig. 6. Lexicality effects in the cortex. Task-related power modulations in word and pseudoword trials and the difference between the two conditions in the three cortical regions of interest: precentral gyrus ($n = 48$), postcentral gyrus ($n = 60$), and superior temporal gyrus ($n = 49$). Clusters with significant power modulations (cluster-based permutation tests, $p < 0.05$) are marked with brown (increases in power) or black (decreases in power) contour. Average times of stimulus presentation, response onset and response offset are marked with vertical black dashed lines (response onset = 0 s).

results of the cluster-based permutation tests revealed 11 sites across 3 subjects showing significant differences between the two conditions primarily in the alpha and beta frequency range (Fig. 7). In one subject, three recording sites in the dorsal part of the precentral gyrus (Fig. 7A, blue circles) showed power decreases in both word and pseudoword trials; however, the decrease in power accompanied a longer time window in the pseudoword trials compared to word trials, resulting in significant power differences between 1 and 2 s before the response onset. This finding aligned with the overall longer reading latencies for pseudowords in this subject. When data were aligned to the stimulus presentation rather than the response onset, the differences were not significant, suggesting that power decreases in this case are related to the production of the stimuli. In another subject, four recording sites (Fig. 7A, purple circles) showed similar differences in the alpha and beta frequency range, with a longer window of power decrease in the pseudoword condition. Notably, four recording sites in the STG (Fig. 7A, green circles) demonstrated a different lexicality effect, with elevated power in the alpha and beta frequency ranges during the production of pseudowords, but not words.

4. Discussion

By using high-resolution LFP recordings from the STN and language related cortical regions (precentral, postcentral, and superior temporal gyri), the present study compared the extent to which processing of pseudowords and words during a reading aloud task can

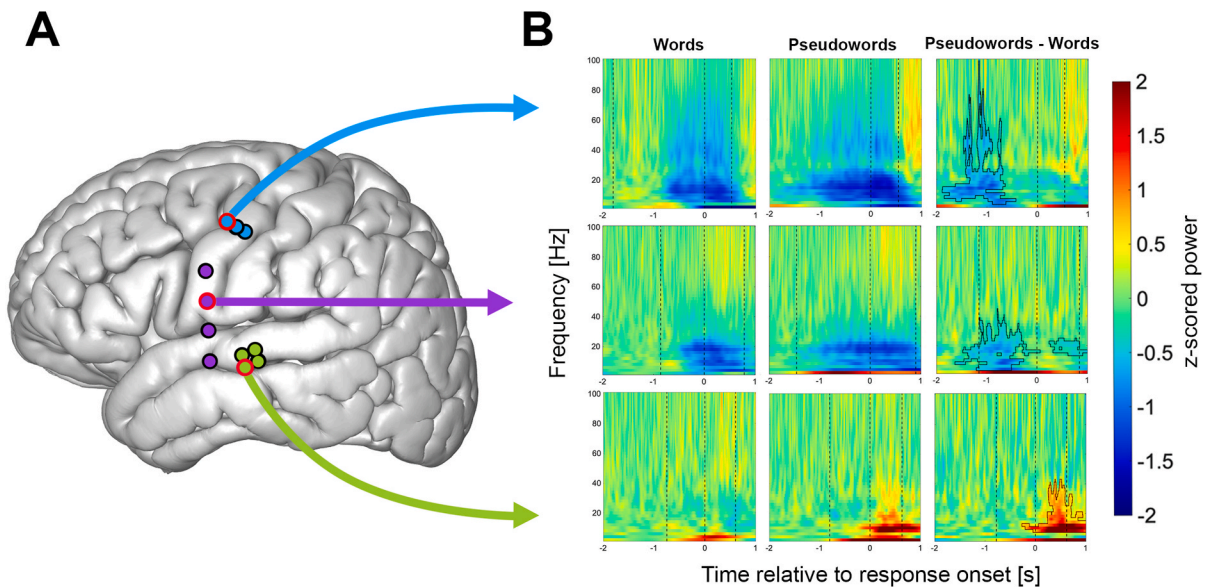


Fig. 7. Lexicality effects at individual cortical recording sites. A) MNI-defined locations of the recording sites showing significant lexicality effects. Each subject's recording sites are marked with a different color. Red lining around circles and color-coded arrows identify sites for which time-frequency resolved power is provided. B) Task-related power modulations in word and pseudoword trials and the difference between the two conditions for the three representative recording sites identified in panel A. Clusters with significant power modulations (cluster-based permutation tests, $p < 0.05$) are marked with brown (increases in power) or black (decreases in power) contour. Average times of stimulus presentation, response onset and response offset are marked with vertical black dashed lines (response onset = 0 s).

be distinguished within the basal ganglia, and how it compares to differences observed in the cortex. We found that reading pseudowords, compared to words, was accompanied by differences in spectral modulation that depended on location, suggesting that the way in which the lexicality effects were instantiated varies with the functional role of the involved brain region.

In the STN, differences in the gamma frequency range (31–70 Hz) distinguished the pseudoword from the word conditions. An overall greater gamma activity was observed in the pseudoword trials, but mixed-effects modeling demonstrated that differences were only significant during the response window. Previously, gamma band activity has been reported across a wide range of brain regions (including the basal ganglia) in the auditory, visual, somatosensory and motor modalities ('sensory gamma response') and has been proposed to serve a perceptual grouping, or 'binding', function, integrating bottom-up information from spatially distributed but temporally coherent electrical signals for the construction of a higher-level representation (Başar, Başar-Eroglu, Karakaş, & Schürmann, 2001; Crone, Korzeniewska, & Franaszczuk, 2011; Engel & Singer, 2001). Increases in gamma power also accompany motor planning and movement (see Cheyne & Ferrari, 2013, for a review), both in the premotor and motor cortex (e.g., Crone et al., 2011, 1998; Szurhaj et al., 2006) and in the STN (e.g., Androulidakis et al., 2007). Thus, observed power modulations in STN gamma activity may serve to functionally bind different neuronal populations involved in the execution and control of the motor activity (e.g., driving the articulator musculature during the production of words and pseudowords). Combined with evidence that subcortical movement-related gamma scales with kinematic parameters (Lofredi et al., 2018), greater gamma activity in the pseudoword trials may reflect the greater articulatory planning and effort required for vocal production of an unknown word, consistent with the idea that the basal ganglia have an important role in motor learning (Turner & Desmurget, 2010).

In addition to bottom-up factors, activity in the gamma frequency band may be strongly modulated by top-down factors, such as memory and attention ('cognitive gamma response') (Başar et al., 2001; Tallon-Baudry et al., 1996; Tallon-Baudry & Bertrand, 1999). For example, the amplitude of the induced gamma may not only depend on low-level stimulus properties (e.g., size, eccentricity, coherence), but may be enhanced due to the attentional selection of sensory information (Tallon-Baudry et al., 1996; Womelsdorf & Fries, 2007). Relevant to language, gamma activity has been hypothesized to reflect associations between words and meanings and the matching of bottom-up acoustic cues to representations stored in short- and long-term memory (Ou & Law, 2018; Pulvermüller et al., 1996). Applied to our data, greater gamma power in the pseudoword condition compared to the real word condition may reflect greater attentional demands and short-term memory costs incurred due to the processing and the subsequent production of unfamiliar, unautomatized letter sequences.

According to a related account, the 'match-and-utilization model' (Herrmann, Munk, & Engel, 2004), bottom-up and top-down factors interact to influence neural synchronization in the gamma band, which subserves both the matching between the stimulus-related information and memory contents, and the utilization aspect of the matching outcome. Utilization in this case may refer to processes such as updating of memory contents, planning and selection of different behavioral responses, reallocating attention, etc. While the match-and-utilization model does not make specific predictions about the brain regions dedicated to such processes, the thalamus and the basal ganglia, including the STN, seem plausible targets due to their ubiquitous feedforward and

feedback connections with the cortex via cortico-striatal-thalamic loops. Thus, according to the utilization hypothesis, greater STN gamma activity in the pseudoword trials compared to word trials in our data may not necessarily indicate lexical processes, but rather executive processes, e.g., inhibition of competing information and habitual responses or switching from automatic to more controlled processing. For example, during the articulation of pseudowords (e.g., 'fape'), subjects have to suppress activation of more familiar real words (e.g., 'fate'), which normally would be co-activated before the spell-out of the pseudoword can be completed. This interpretation is in line with existing data showing a correlation between STN gamma activity and switching costs for different phonetic and semantic categories during a verbal fluency task (Anzak et al., 2011) and the correlation of STN gamma activity and subjects' performance on the random number generation task, in which they have to suppress the more automatic, ordered counting (Anzak et al., 2013). Thus, the role of the STN during word processing could be to contribute to the emergence of a specific behavior from competing behavioral plans (Frank, 2006; Redgrave, Prescott, & Gurney, 1999).

Turning to the cortical data, it should be acknowledged that the cortical areas traditionally implicated in lexical processing, such as the left fusiform gyrus and the inferior frontal gyrus, were not sampled in this subject cohort. This may partly explain why word-pseudoword differences were observed only in 11 recording locations. Nevertheless, clusters with significant power differences between word and pseudoword conditions were noted in the precentral, postcentral and superior temporal gyri in the group analysis (Fig. 6), although in the LMEM analysis differences between words and pseudowords remained significant only in the alpha and beta frequency ranges in the precentral gyrus. Power decreases slightly before and during the production of pseudowords were also observed at 7 individual recording sites (mostly in the precentral gyrus) in the low beta and alpha frequency bands (Fig. 7). Desynchronization of activity in the beta (and sometimes also alpha) band over sensory and motor areas is a well-known neural signature of preparation and execution of a voluntary movement (for review, see Engel & Fries, 2010; Piai & Zheng, 2019; Weiss & Mueller, 2012). In language studies, a desynchronization of beta activity has been repeatedly demonstrated during overt movement (e.g., word generation) (Singh, Barnes, Hillebrand, Forde, & Williams, 2002) and even covert, or imaginary, movement (e.g., processing of action verbs) (van Elk, van Schie, Zwaan, & Bekkering, 2010). Based on this evidence, greater desynchronization of alpha-beta activity in the precentral gyrus during pseudoword trials may suggest a stronger motor preparation and motoric effort involved in the production of novel speech sequences compared to real words for which speech motor programs should be robust and automatized.

Interestingly, a different pattern of activity in response to the lexicality manipulation was observed at four other recording sites located in the mid-STG region. These sites produced an increase rather than a decrease in alpha-beta power for pseudoword stimuli. The timing of this effect was peculiar — robust alpha-beta increases for pseudowords were elicited during the spoken response but were most prominent around speech offset (Fig. 7). According to Engel and Fries (2010), decreases in beta activity should be expected in paradigms where the behavioral response is largely determined by bottom-up factors, while increases in power may be associated with endogenous, top-down components. Taking into account that modulations of alpha-beta activity have been implicated in attentional processes (for review, see Klimesch, 2012), and that feedback control appears to be established dynamically by oscillations in the alpha-beta bands (Halgren et al., 2019; Michalareas et al., 2016; van Kerkoerle et al., 2014), the observed increase of power around alpha and beta frequencies at the offset of pseudoword productions may reflect greater attentional and self-monitoring costs associated with the uncertainty of producing novel, unfamiliar stimuli. Indeed, the STG has been proposed to play a role in the auditory feedback control system (Guenther et al., 2006) and the self-monitoring network (Indefrey, 2011): it takes the speaker's own voice as input and matches it with the phonological score stored in memory. The involvement of the STG in self-monitoring is also suggested by studies using real-life perturbations of subjects' own speech (McGuire, Silbersweig, & Frith, 1996; Tourville, Reilly, & Guenther, 2008). Thus, linking the functional relevance of alpha and beta activity in attention with the function of the STG in feedback and self-monitoring, it is possible that the observed power increases at STG sites index a mechanism whereby one's own spoken response is evaluated against the intended output. Of note, some neuroimaging studies also report greater activity for pseudowords compared to words in the STG region, if the stimuli are presented auditorily (Kotz et al., 2002; Raettig & Kotz, 2008).

5. Limitations

Particular limitations of the study must be noted. Provided that opportunity to record directly from the STN arises very rarely and is restricted to diseased populations, the clinical state of our patient cohort may potentially impact the results. Additionally, the specific placement of the ECoG strips through the burr hole leads to sparse coverage of some cortical regions, precluding evaluation of the dynamics of lexical processing across the entire cortex. Surprisingly, the reported lexicality effect was observed only in a small portion of the cortical data (11 out of 157 cortical recording sites), which we attribute either to individual and functional anatomic variability across patients or to lack of power. It should also be noted that while a reading aloud task involves an overt motor behavior (i.e., speaking), we did not separately control for the motor aspects of response generation due to the time constraints on the administration of the protocol in the operating room. This makes it potentially difficult to separate lexical and motoric contributions to the observed results. Finally, we interpret the results in association with the existing literature on the functional relevance of the modulations of the neural signal in the traditional EEG frequency bands. Neural band modulations have been implicated in various cognitive processes, and we acknowledge that the reading aloud task necessarily invokes multiple mental computations.

6. Conclusions

Language is classically considered to be subserved by cortical regions. We employed a novel experimental paradigm in awake, speaking patients undergoing STN-DBS for Parkinson's disease, where LFPs were simultaneously recorded from the STN and the cortex. This allowed us to compare neural activity in the STN and cortical regions during reading aloud of real words and pseudowords.

We found that STN and cortical activity is significantly modulated during a spoken response, but that the lexicality effect is differentially instantiated in the two brain regions. In the STN, gamma band activity (31–70 Hz) was significantly greater during processing of pseudowords than words. In the cortex, stronger decreases in the beta frequency band were observed for pseudowords in the precentral gyrus. Additionally, lexicality effects in cortical alpha and beta band activity were present at individual cortical sites with varying temporal and topographic characteristics. While this study has exploratory nature, it represents a step forward to understanding the role of the STN (and the basal ganglia) in language processing and provides insights that can be used to generate hypotheses for future studies.

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Footnotes

1. Data from a subset of subjects ($n = 11$) has been previously used to examine STN encoding of speech articulators in Chrabaszcz et al. (2019). Unlike the previous analysis, the current analysis is based on a smaller number of trials per recording session ($n = 60$ instead of 120) because only the first 60 trials were balanced for presentation of words and pseudowords. Trial inclusion criteria also differed between the two datasets due to different research questions. Additionally, recordings from the STG were added to the current dataset, but were absent in the previously reported data.

Declaration of competing interest

The authors declare no competing financial interests.

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