Frequency-specific brain dynamics related to prediction during language comprehension

Kristijan Armeni*[1], Roel M. Willems[1,2], Antal van den Bosch[2,3] and Jan-Mathijs Schoffelen[1]

[1]Donders Institute for Brain, Cognition and Behaviour, Radboud University, Nijmegen, The Netherlands

[2]Centre for Language Studies, Radboud University, Nijmegen, The Netherlands

[3]Meertens Institute, The Royal Netherlands Academy of Arts and Sciences, Amsterdam

Abstract

The brain's remarkable capacity to process spoken language virtually in real time requires fast and efficient information processing machinery. In this study, we investigated how frequency-specific brain dynamics relate to models of probabilistic language prediction during auditory narrative comprehension. We recorded MEG activity while participants were listening to auditory stories in Dutch. Using trigram statistical language models, we estimated for every word in a story its conditional probability of occurrence. On the basis of word probabilities, we computed how unexpected the current word is given its context (word perplexity) and how (un)predictable the current linguistic context is (word entropy). We then evaluated whether source-reconstructed MEG oscillations at different frequency bands are modulated as a function of these language processing metrics. We show that theta-band source dynamics are higher in high relative to low entropy states, likely reflecting lexical computations. Beta-band

*k.armeni@donders.ru.nl

dynamics are increased in situations of low word entropy and perplexity possibly reflecting maintenance of ongoing cognitive context. These findings lend support to the idea that the brain engages in the active generation and evaluation of predicted language based on the statistical properties of the input signal.

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1 Introduction

The brain's remarkable capacity to process spoken language virtually in real time requires fast and efficient information processing machinery. The efficiency of the brain network for language might in fact rely partially on its ability to dynamically generate predictions from, and apply them to the incoming linguistic signal. In recent years, numerous theoretical accounts of brain function have emphasized the capacity of the brain to use its ongoing contextual embedding for anticipating the future states of environment and the outcomes of its own actions (Bar, 2009; Clark, 2013; Friston, 2005).

The notion of prediction in the brain and probabilistic processing under uncertainty has received increased attention in domains such as memory, perception, and decision-making (Bach & Dolan, 2012; den Ouden, Kok, & de Lange, 2012; Hasson, 2017; Pouget, Beck, Ma, & Latham, 2013). Probabilistic predictive computations in language comprehension, however, have proven to be notoriously elusive to operationalize. As a consequence, the term "prediction" has received differing interpretations in the broader community (Huettig & Mani, 2016; Kuperberg & Jaeger, 2016). In the current study, we turn to computational linguistics, specifically probabilistic language models and information theory, which provide a principled framework for operationalizing predictions in language comprehension as expectation-based processing.

A language model is an estimate of a probability distribution over words in a sentence given a fixed number of words seen so far. Specifically, trigram models used presently estimate the probability of the current word's occurrence based on the two words just seen. From estimates of probabilities, it is straightforward to compute information-theoretic measures—word perplexity (surprisal) and word entropy—that quantify the amount of information-processing work (in the sense of Shannon information) performed by the cognitive system in transitioning from one word to the next in the narrative (see Hale, 2016, for a recent review). Recently, information-theoretic metrics have been tested against neuro-imaging data to explore whether there is support for the idea that the brain might use statistics of the input implicitly to generate and evaluate predictions for efficient

processing.

Work using fMRI has delineated the neural correlates of information-processing metrics in brain regions. In a study by Willems, Frank, Nijhof, Hagoort, and van den Bosch (2016), word entropy was shown to be negatively related to hemodynamic responses in the right inferior frontal gyrus, the left ventral premotor cortex, left middle frontal gyrus, supplementary motor area, and the left inferior parietal lobule, whereas word surprisal showed positive relationship bilaterally in the superior temporal lobes and in a set of (sub)cortical regions in the right hemisphere. Henderson, Choi, Lowder, and Ferreira (2016) have shown that syntactic surprisal is related to activity in the left inferior frontal gyrus and in the left anterior temporal lobes during natural story reading. Lopopolo, Frank, van den Bosch, and Willems (2017) further showed that fluctuations in part-of-speech, word, and phoneme perplexity during auditory narrative comprehension are related to largely separated brain activity in the temporal, inferior parietal and perisylvian cortical areas.

Electrophysiological methods are beginning to shed light on spectro-temporal neural correlates of probabilistic models. Word surprisal has been shown to correlate with the EEG N400 amplitude, a well-known marker of language processing, during sentence reading (Frank, Otten, Galli, & Vigliocco, 2015). In a recent ECoG study, Nelson, Karoui, et al. (2017) showed that bigram word entropy during sentence reading is negatively related with fluctuations in the high gamma (70–150 Hz) power on electrodes overlying left posterior temporal regions. In a separate analysis of the same dataset, entropy reduction (changes in word-by-word syntactic uncertainty) was found to have a positive linear relationship with high gamma power in the left anterior and posterior inferior temporal electrode sites (Nelson, Dehaene, Pallier, & Hale, 2017).

Although fMRI work provided insights into spatial fingerprints of probabilistic computations and work in electrophysiology showed their temporal and high-frequency neural characteristics during sentence reading, it is as of yet unclear whether these statistical quantities are also reflected in ongoing electrophysiological activity during natural language listening. How are word-by-word

context-dependent probabilistic predictions reflected in brain dynamics during naturalistic story comprehension?

To address this question, we recorded MEG during auditory story comprehension and used probabilistic language models to quantify the amount of information conveyed by each heard word (word perplexity) and the uncertainty as to what word(s) will likely follow up the current word (word entropy) (see figure 1, panel A). We then compared the power of frequency-specific MEG neural source dynamics as a function of high and low perplexity and entropy states. We focused on dynamics in the theta, alpha, beta, and gamma frequency ranges as these have been previously implicated in core linguistic computations (see M. Bastiaansen & Hagoort, 2006; Lewis & Bastiaansen, 2015; Weiss & Mueller, 2012, for reviews).

Figure 1: Design and data analysis. A) We recorded MEG responses while participants listened to auditory stories (excerpts from novels recorded as audiobooks). From the acoustic signal, word onsets were automatically identified. For each individual word in a story, we computed a complexity score (word perplexity or entropy) on the basis of trigram language model probabilities. B) Full story datasets were cut (epoched) into 0.5 second long snippets. On the basis of the average complexity within each snippet, we assigned the snippets into high and low complexity bins. We then compared frequency-specific power of MEG source activity in the corresponding complexity bins.

2 Methods

2.1 Participants and data acquisition

We recruited 25 healthy left- or right-handed (see Willems, Haegen, Fisher, & Francks, 2014, for inclusion justification) participants (13 female, mean age 25.8 ± 7.6 [$M \pm SD$]). Participants gave informed consent and were financially compensated for their participation. The study was approved by the "Committee

on Research Involving Human Participants" (CMO) in the Arnhem—Nijmegen region and followed the guidelines of the Helsinki declaration. Participants received monetary compensation for the participation.

We collected MEG data with a 275 axial gradiometer system (CTF) in seated position at the Donders Centre for Cognitive Neuroimaging in Nijmegen, The Netherlands. The signals were digitized at a sampling frequency of 1200 Hz. Three coils were attached to the participant's head (nasion, left, and right ear canals) to determine the position of the head relative to the MEG sensors. Throughout the measurement, the head position was continuously monitored using custom software (Stolk, Todorovic, Schoffelen, & Oostenveld, 2013). During breaks, the participant was allowed to reposition to the original position if needed. Participants were able to maintain a head position within 5 mm of their original position. Three bipolar Ag/AgCl electrode pairs were used to measure the horizontal and vertical electro-oculogram, and the electro-cardiogram.

2.2 Experimental procedure and stimulus materials

In the present analysis, we combined two sets of recordings of in total 25 participants (7 from the first set and 18 from the second set). In both datasets, participants listened to the same short stories in Dutch. The number of heard stories for the first ten subjects varied from 6 to 8. All subjects in the second dataset heard 5 stories. All subjects were instructed to listen to stories attentively for comprehension. The 18 subjects of the second dataset were additionally informed that they would answer two short multiple choice comprehension questions after each story (see Appendix A). They responded to comprehension questions by means of a button press.

Each story was presented binaurally via a sound pressure transducer through two plastic tubes terminating in plastic insert earpieces. A black screen was maintained while participants listened to the stories. Presentation of the auditory stories was controlled with Presentation software (version 16.4, NeuroBehavioral Systems Inc.). During story listening, participants were looking at a black screen and were not otherwise constrained.

The auditory stories were obtained from the subcorpus of Dutch literary stories available in the Spoken Dutch Corpus, "Corpus Gesproken Nederlands" (Oostdijk, 2000). The recordings were excerpts (mostly chapters) from audiobooks that were originally produced for Dutch Libraries for the Blind. The excerpts were spoken at a normal rate, in a quiet room, by different speakers (one speaker per story). The details for each of the stories are reported in Table 1.

story	duration (mm:ss)	num. words	num. sentences	avg. sentence length
1	03:44	518	33	15.7
2	03:58	649	42	15.5
3	12:46	1730	131	13.2
4	03:59	657	35	18.8
5	07:55	1320	68	19.4
6	08:02	1127	87	13
7	04:03	549	34	16.1
8	08:04	999	62	16.1

Table 1: The number of words tokens, number of sentences and number of words per sentence for each of the stimulus stories.

2.3 N-gram language models

Word probabilities were estimated with a trigram language model, also known as a third order Markov model. A trigram language model estimates the probability P of the current word's occurrence conditioned on the past two words in the sentence:

$$P(w_t) = P(w_t \mid w_{t-2}, w_{t-1}) \tag{1}$$

The stories were tokenized with the Frog natural language processing toolkit (Bosch, Busser, Canisius, & Daelemans, 2007). Language models for word entropy and perplexity estimates were then computed using the SRILM (Stolcke, 2002) and WOPR (van den Bosch & Berck, 2009) software packages, respectively. The model was trained on a selection of 10 million sentences (comprising 197 million word tokens; 2.1 million types) from the Dutch Corpus of Web, NLCOW (Schäfer & Bildhauer, 2012).

2.3.1 Lexical perplexity

High word perplexity values indicate that the currently encountered word was less expected given the context. In psychological terms, perplexity is a "backward-looking" metric in that it models the degree of listener's surprise upon encountering the word (higher perplexity means higher surprise) and the amount of information processing work required (higher surprise requires more information processing) given the past context. Perplexity is mathematically related to the information-theoretic measure of surprisal which is defined as the negative logarithm of the word's conditional probability of occurrence:

$$surprisal(w_t) = -\log P(w_t \mid w_{t-2}, w_{t-1}) \tag{2}$$

Perplexity is defined as the exponential transformation of surprisal:

$$perplexity(w_t) = 2^{surprisal(w_t)} = 2^{-\log P(w_t|w_{t-2},w_{t-1})} \tag{3}$$

2.3.2 Lexical entropy

Word entropy quantifies uncertainty in the probability distribution of possible upcoming words. High entropy signifies that there are many possible words that can follow the current word, whereas low entropy indicates that there are only few, highly probable words that can complete current sentence position. In other words, word entropy is a "forward-looking" metric and models the degree of the listener's or reader's uncertainty about the upcoming word given the words encountered so far. Entropy for the current word position is defined as the information-theoretic chaos in the distribution of all possible upcoming words at $t+1$ given the words encountered so far $(w_{1,...,t})$:

$$entropy(t) = -\sum_{w_{t+1} \in W} P(w_{t+1} \mid w_1, ..., w_t) \log P(w_{t+1} \mid w_1, ..., w_t) \tag{4}$$

where W denotes the set of possible words following $(w_{1,...,t})$.

We used base-2 logarithm as the scaling factor, therefore both perplexity and entropy are expressed in bits. A descriptive visualization for word perplexity and word entropy along with two control variables (lexical frequency and word duration) is provided in figure 2. Along the diagonal, the matrix shows distributions for word entropy, perplexity, lexical frequency, and word duration (msec) per story. Distributions for lexical perplexity and lexical frequency have been log 10-rescaled for visualization purposes. Lower off-diagonal panels display scatterplots for combinations of variables. The corresponding upper off-diagonal panels show the corresponding Pearson correlation coefficient between variables.

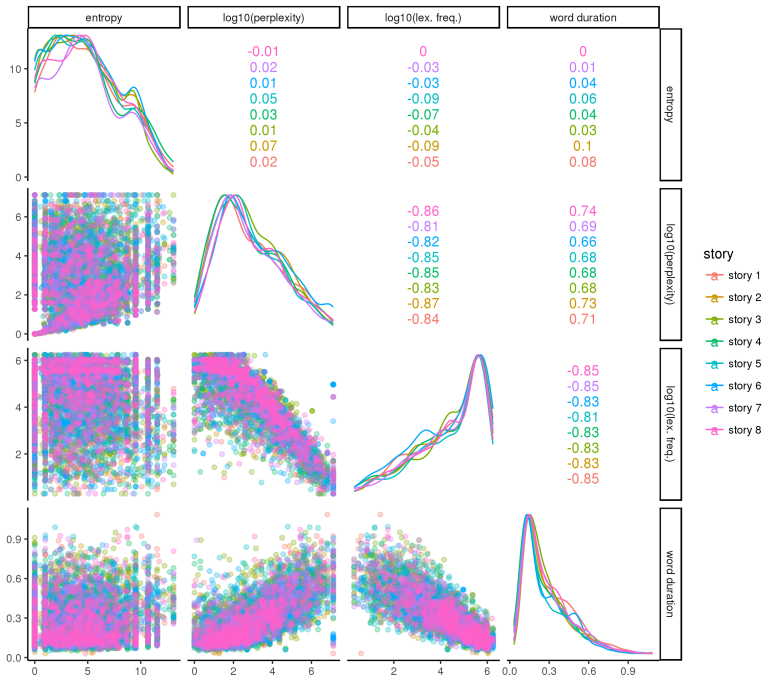

Figure 2: Scatterplot matrix for entropy, log10-transformed perplexity, log10-transformed lexical frequency, and word duration (msec) per story. Color-coding represents data for individual stories. Values in the upper off-diagonal panels are story-specific Pearson correlations coefficients for the corresponding variable pair. On the diagonal are story-specific density plots for the corresponding variable. Lower off-diagonal panels show scatterplots for the corresponding variable pair. R code to reproduce the figure: `figure_2.R`

2.4 Preprocessing

The analysis of MEG data was performed in MATLAB, version 2016b (Mathworks, Inc.) with the FieldTrip software package (Oostenveld, Fries, Maris, & Schoffelen, 2011), together with a custom in-house MATLAB code. The complete code with documentation used in the analysis with cursory documentation is available at: https://github.com/KristijanArmeni/dyncon_streams/tree/master.

2.4.1 MEG

Prior to preprocessing, the raw data were demeaned. We then applied notch filtering at the bandwidth of 49–51, 99–101, and 149–151 Hz to remove the potential line noise artifacts. Artifacts related to muscle contraction and squidjumps were identified and removed using a semi-automatic artifact rejection procedure (http://www.fieldtriptoolbox.org/tutorial/automatic_artifact_rejection). The data were then downsampled to 300 Hz. MEG components reflecting eye-blinks were estimated using the FastICA algorithm (https://research.ics.aalto.fi/ica/fastica/) as implemented in Fieldtrip functionalities. Relevant components were identified based on their topography and time-courses and removed from the data.

2.4.2 MRI

Original volumes of T1-weighted MRI images of each participant were manually co-registered to the MNI headspace coordinate system. MRI images were then re-sliced to an isomorphic $256 \times 256 \times 256$ space and co-registered to the MEG (CTF) headspace coordinate system by defining the positions of pre-auricular points and the nasion MEG coil on the re-sliced MRI images. To reproduce and localize the position of the left and right pre-auricular points on the MRI images, we placed custom-made markers (vitamin E capsules) in participants' ear molds during MR image acquisition (see http://www.fieldtriptoolbox.org/faq/how_are_the_lpa_and_rpa_points_defined). To make the co-registration as precise as possible, we used the same ear molds as in the MEG session. No specific marker, other than anatomical identification on the image, was used to localize the nasion coil.

After co-registration, the Brain Extraction Tool (BET; S. M. Smith, 2002) from the FSL command-line library (v5.0.9; Jenkinson, Beckmann, Behrens, Woolrich, & Smith, 2012) was used to delete the non-brain tissue (skull stripping) from the whole head. To obtain a description of individual subject's cortical sheet, we performed cortical surface reconstruction with the Freesurfer image analysis suite, which is documented and freely available for download online

(http://surfer.nmr.mgh.harvard.edu/), using the surface-based stream implemented in the `recon_all` command-line tool. The post-processing of the reconstructed cortical surfaces was performed using the Connectome Workbench `wb_command` command-line tools (v1.1.1; https://www.humanconnectome.org/software/workbench-command).

2.4.3 Audio

The onsets of the acoustic signals from audio stories were first corrected for the delay with respect to the MEG triggers. We then computed the amplitude envelope of auditory signals following Gross et al. (2013). Using the Chimera toolbox (http://research.meei.harvard.edu/chimera/More.html, see also Z. M. Smith, Delgutte, & Oxenham, 2002), we constructed 10 frequency bands of equal width in the range 100–10,000 Hz to match the frequency range of human hearing along the basilar membrane. The power envelopes of each of the constructed frequency bands were averaged together to yield a single auditory power envelope. This averaged auditory envelope was used in computation of audio–MEG coherence (see Section 2.7.3) and as confounding variable in the analysis of linguistic variables (see Section 2.7.2).

2.5 Epoching and linguistic information content

The pre-processed MEG data were re-epoched into 0.5 second-long time segments (see figure 1, panel B). Aligned with recorded MEG time series, we logged the timing of word onsets and offsets and the word's entropy and perplexity values. Since an individual epoch could straddle several words (our epoching step did not consider word boundaries), we computed, for each epoch, the mean over individual word perplexity and entropy values weighted by the individual word's duration (such that longer words contributed more to the overall mean complexity score). This step resulted in a point estimate of linguistic complexity in each epoch.

The distribution of all epoch-specific complexity values was subsequently binned into low and high complexity bins which contained entropy or perplexity

scores below the 33- and above the 66-quantiles, respectively (see figure 1, panel B, third sub-figure). The two linguistic complexity bins served as the contrast for our comparison of frequency-specific MEG source power (see section 2.8).

2.6 Temporal lagging of MEG time-series

An important caveat of the procedure described so far is that, despite temporal smoothing due to the averaging step per epoch, it assumes quasi-instantaneous effects of linguistic features on MEG dynamics (e.g. a word's unexpectedness is assumed to be observed at time of word onset in MEG time-series). To adjust for this, we repeated the epoching procedure 3 times, each time with temporally lagged versions of MEG signals relative to the time course of linguistic information. That is, prior to epoching, we selected the MEG time-series starting 200, 400, and 600 msec post-onset and realigned them with the onset of the original language time-series. Temporal shifting of the estimated power envelopes relative to the linguistic features allowed us to investigate the temporal dynamics of the association between oscillatory power and the linguistic features, accounting for a likely delay between the word onset and the modulatory effect of the linguistic feature on the brain response.

2.7 Source reconstruction

The cortical sheet reconstruction procedure (see section 2.4.2) resulted in a description of individual subjects' locations of potential neural sources along the cortical sheet (source model) with 7,842 source locations per hemisphere. We used a single-shell spherical volume conduction model (head model) based on a realistic shaped surface of the inside of the skull (Nolte, 2003) to compute the forward projection matrices (leadfields).

We performed "dynamic imaging of coherent sources" (Gross et al., 2001), a frequency-domain spatial filtering technique, to estimate the frequency-specific single-trial audio-MEG coherence and MEG neural source power on the reconstructed cortical sheets. To estimate frequency-resolved coherence spectra we used linearly constrained minimum variance spatial filtering (LCMV, Veen,

Drongelen, Yuchtman, & Suzuki, 1997). Both methods can be deployed with the Fieldtrip "ft_sourceanalysis" routine.

2.7.1 Neural source power

The cross-spectral density of the sensor-level data was first computed by estimating the single-trial Fourier power per frequency of interest. The dpss multitaper method with progressively larger smoothing windows (2 Hz for theta and alpha bands; 5 for beta bands; and 15 for gamma bands) was used to estimate the power at the following frequency ranges: theta (4–8 Hz; centered at 6 Hz), alpha (8–12 Hz; centered at 10 Hz), low beta (11–21 Hz; centered at 16 Hz), high beta (21–31 Hz; centered at 26 Hz), low gamma (30–60 Hz; centered at 45 Hz), and high gamma (60–90 Hz; centered at 75 Hz) frequency bands. The Fourier spectra were subsequently converted to bi-variate cross-spectral densities.

The subject-specific leadfields (see section 2.4.2) and cross-spectral densities were then used to estimate the inverse spatial filters (beamformers). The lambda regularization parameter was specified as 100%. This step resulted in a spatial filter for each source location on the cortical sheet. The sensor level single-trial (MEG channel-by-trial) Fourier-transformed power data were then left-multiplied with the location-specific spatial filter (source dipole moment-by-MEG channel) to yield the trial-specific estimate of source power at that location.

2.7.2 Confounding variables

Initial exploration of our independent variables shows that our trigram word perplexity is negatively related with word lexical frequency (see figure 2). That is, the model assigns higher perplexity scores on average to words that occur less frequently in the corpora. We therefore decided to treat mean log-transformed lexical frequency per epoch as a potential confounding variable in our analysis. Word frequency counts were obtained from the SUBTLEX corpus (Keuleers, Brysbaert, & New, 2010).

In addition, to remove the part of the variance in the estimated MEG oscil-

latory activity that is due to purely low-level acoustic fluctuations in the input signal, we included epoch-averaged auditory envelope power (see section 2.4.3) as a potential confound as well. Prior to computing the statistical contrast described in section 2.8, the variance attributed to lexical frequency and auditory envelope fluctuations was estimated by means of a general linear model and was regressed out from the power spectra (see Stolk et al., 2013, for details).

2.7.3 Audio envelope–MEG source coherence

To estimate the coherence between averaged audio envelope and source neural dynamics, we first computed a complex Fourier representation of the sensor level signals per epoch centered at the frequency of interest. The Fourier spectra were subsequently converted to bi-variate cross-spectral densities. The subject-specific leadfields (see section 2.4.2) and cross-spectral densities were then used to estimate the inverse spatial filters (beamformers). The lambda regularization parameter was specified at 100%, which reflects a diagonal loading of the co-variance matrix with the mean of the variance across channels.

2.7.4 Frequency-resolved audio envelope–MEG source coherence

To estimate audio-cortico coherence across a broader spectrum of frequencies, we used the LCMV approach, a time-domain beamformer algorithm. The story-epoched MEG time-series were first re-epoched to 4s-long time windows. We then computed the sensor-level co-variance matrix that was used in the LCMV algorithm to estimate the beamformer weights. The lambda regularization parameter to "ft_sourceanalysis" routine was specified at 100%.

Given that the cortico-audio coherence is typically found in areas surrounding primary auditory cortices (e.g. Gross et al., 2013), we only computed spatial filters for areas BA42 as defined the Conte69 atlas (brainvis.wustl.edu/wiki/index.php//Caret:Atlases/Conte6 Atlas), which provides a parcellation of the neocortical surface based on Brodmann's cytoarchitectonic atlas, consisting of 41 labeled parcels per hemisphere. The sensor-level time-series were then projected to the source space by left-multiplying them with location-specific beamformer weights.

Using the dpss multitaper method with a smoothing window of 1 Hz, we computed the complex Fourier representation of the time-domain audio and MEG source signals in the range between 0 and 50 Hz which was used to compute the coherence spectrum per frequency band.

2.8 Within subject contrast

An independent two-samples t-statistic was used to quantify differences in mean neural source power between high and low complexity levels per each of the six frequency bands in every subject. The t-statistic was used in order to normalize for potential signal-to-noise differences in MEG signals between the two groups not related to the comparison of interest. This step resulted in a t-map (a number-of-source-locations by number-of-time-lags matrix of t-values) for every subject and frequency band.

2.9 Group contrast and inference

The subject-specific t-statistics computed in the first-level step were entered into a group-level analysis. The dependent-samples t-statistic was computed for every pair of source-location and time-point where the first sample consisted of observed per-subject independent-samples t-statistics from the first-level analysis, and the second sample consisted of a matrix of same dimensions than that sample 1 but filled with zeros instead of observed t-statistics.

Statistical significance of observed group differences was determined by means of the cluster-based non-parametric permutation test (Maris & Oostenveld, 2007). Here, the goal is to determine whether the global (i.e. pertaining to differences across all source and time-points) null hypothesis can be rejected by first clustering the observed samples (i.e. sample points represented by dependent samples t-statistics), computing a cluster statistic per cluster and comparing our observed cluster statistics to a reference permutation distribution of cluster statistics. Sample-specific t-statistics that exceeded the alpha level of 0.05 were clustered according to adjacency (in the spatial and temporal domains).

For each formed cluster, the cluster-level statistic was calculated by sum-

ming the sample-specific t-statistics belonging to a cluster. Next, to test the observed cluster t-statistics, a reference distribution was computed. This distribution was created by permuting (randomly exchanging) data between the conditions, and then calculating the maximal positive and negative cluster t-statistic for each permuted data set. The permutation step was repeated 1,000 times. Finally, the observed t-statistic was tested against the reference distribution. The observed t-statistic was considered significant if it was located beyond the determined alpha threshold of .025 on the negative or positive end of the reference distribution. The permutation test controls for multiple comparisons in space and time.

3 Results

3.1 Comprehension questionnaires

The subjects who had to answer the comprehension questions (see section 2.2) all correctly responded to at least 7 or more (out of 10) comprehension questions showing that they did pay attention to the contents of the narratives.

3.2 Language model contrasts

We compared the band-limited MEG signal power in high and low entropy and perplexity bins (see section 2.5) in 6 frequency bands (theta, alpha, low-beta, high-beta, low-gamma, high-gamma).

3.2.1 Word perplexity

Comparison between high and low perplexity epochs across frequencies showed that there was a statistically significant difference in MEG power for the low beta (permutation p-value = 0.046) and high beta (permutation p-value = 0.006) bands. Differences for both the low and high beta-bands showed negative direction (figure 3, panels A and B) of the effect, meaning that, on average, highly surprising words in the narrative were accompanied by lower beta-band power relative to expected, unsurprising words.

For both frequency bands, the effects are predominantly left-lateralized with peaks over left central, temporal and frontal areas. Power differences progressively increase with each subsequent temporal lag peaking at the lags of 400 and 600 msec.

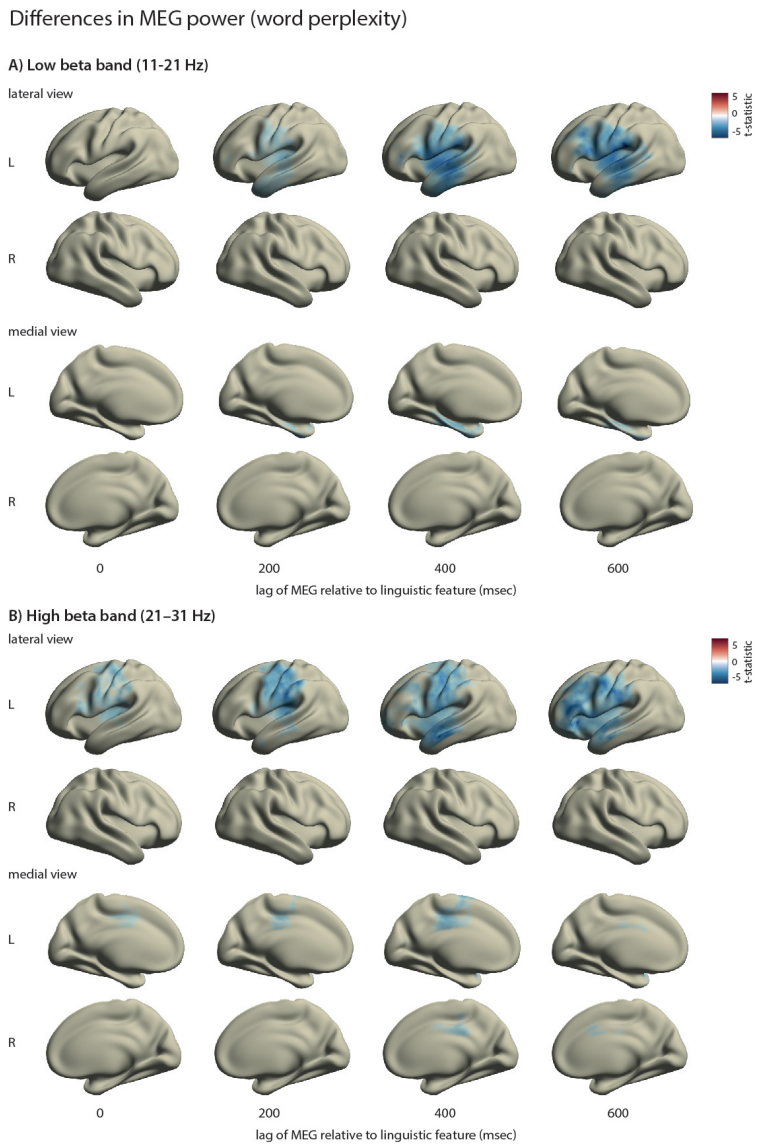

Figure 3: Group level t-maps for low beta (11–21 Hz, panel A and high beta band (21–31 Hz, panel B) power quantifying differences between high and low perplexity bins. Source maps show paired-samples t-statistic per source location and time lag where the upper and lower extreme point of the color bar are determined by the maximal absolute value over t-statistics and its negative, respectively. For the purposes of visualization, displayed are only t-statistics for source locations belonging to the permutation cluster with the highest cluster statistic, that is, source locations not belonging to the maximal clusters the cluster are set to a value of zero. MATLAB code to reproduce source maps: `script_sourceplot4eps.m`

3.2.2 Word entropy

Comparison between high and low entropy epochs showed that there was a statistically significant difference in the theta (permutation p-value = 0.016) and the low beta bands (permutation p-value = 0.024). Power differences in the theta-band showed a predominantly positive direction (red color coding in figure 4, panel A) showing that high entropy contexts, which are less predictive about upcoming words, are on average accompanied by higher theta-band power compared to more predictive, low entropy contexts.

Theta-band power showed left-lateralized differences with focal maxima over the middle temporal and inferior frontal lobes (red color coding in figure 4, panel A, upper). We additionally localized differences to medial cortical areas with focal peaks in the bilateral posterior cingulate cortex and posterior medial temporal areas, right anterior cingulate cortex, and left inferior parietal cortex. (figure 4, panel A, lower).

Differences in the low beta-band revealed predominantly negative difference (blue color coding in figure 4, panel B) meaning that in high entropy contexts beta-band power was on average lower relative to more predictive, low entropy contexts. The spatial structure of observed group-level beta-band differences across time lags shows a predominantly left-lateralized peak difference over left central areas and superior temporal areas extending to angular gyrus. Inspecting the temporal structure of the effect, differences are most pronounced when the MEG signal is lagged relative to the linguistic feature by 600 msec.

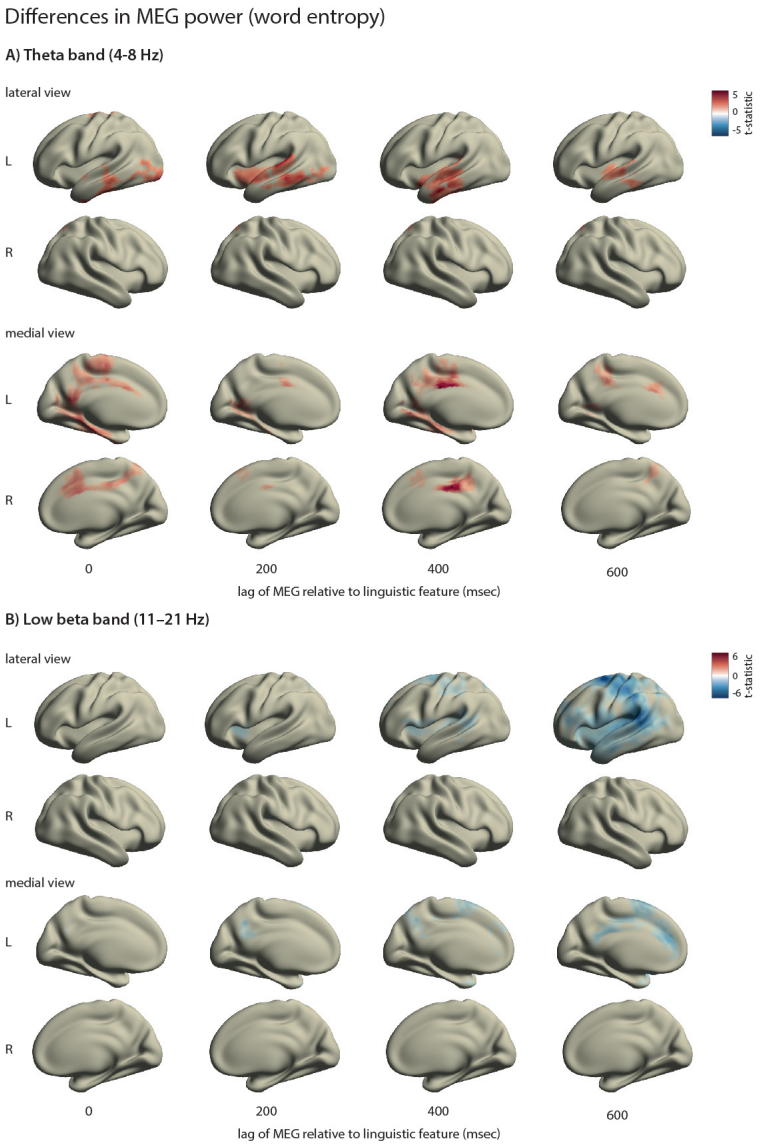

Figure 4: Frequency-specific power differences between conditions visualized here as group-level t-maps for theta-band (4–8 Hz, panel A) and lower beta-band (11–21 Hz, panel B) power quantifying differences between high and low entropy bins. Source maps show paired-samples t-statistic per source location and time lag where the upper and lower extreme point of the color bar are determined by the maximal absolute value over t-statistics and its negative, respectively. For the purposes of visualization, displayed are only t-statistics for source locations belonging to the permutation cluster with the highest cluster statistic, that is, source locations not belonging to the maximal clusters the cluster are set to a value of zero. MATLAB code to reproduce source maps: `script_sourceplot4eps.m`

3.3 Audio envelope–MEG coherence

To additionally ascertain that our entropy-theta effect is not driven by the relationship between acoustic envelope fluctuations and MEG power spectrum we, as a control analysis, explored the topography of this effect in our dataset. This phenomenon, also known as "speech entrainment", has been extensively reported in studies using auditory sentences or narratives as stimuli (Ahissar et al., 2001; Giordano et al., 2017; Gross et al., 2013; Lam, Hultén, Hagoort, & Schoffelen, 2018; Luo & Poeppel, 2007; Park, Ince, Schyns, Thut, & Gross, 2015).

We computed coherence between the source reconstructed MEG time-series and speech envelope fluctuations. The spatial distribution of average audio envelope-MEG coherence for the theta band is displayed in figure 5, panel A. Panel B shows the audio envelope-MEG coherence spectra (individual participants in grey) for the left and right BA42. This analysis confirms earlier reports of right hemispheric group-average lateralization of theta-band entrainment to the speech envelope (Lam et al., 2018), as well as the variability across participants.

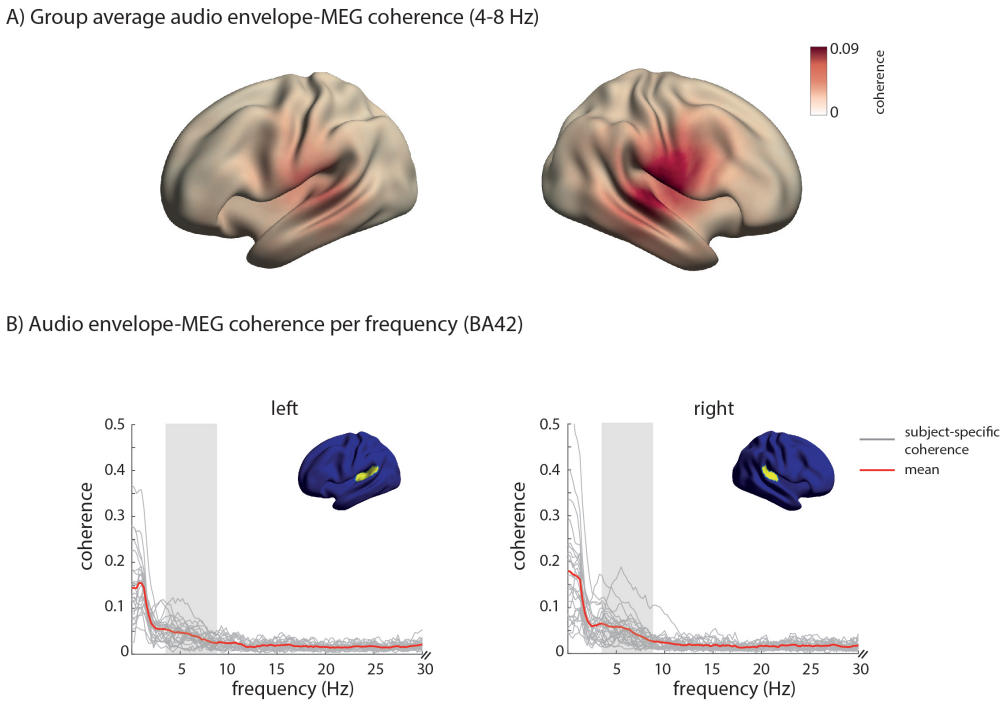

Figure 5: Audio envelope–MEG coherence quantifying entrainment of low-frequency MEG power by auditory envelope fluctuations. A) Coherence between auditory envelope and MEG signals in theta band. Visualized are coherence values averaged across subjects. Coherence is bounded between 0 and 1. B) Coherence between auditory envelope and MEG signals across the frequency spectrum in the 1–50 Hz range (shown up to 30 Hz) in the left (left panel) and right BA42 (right panel). Grey lines show median BA42 audio-MEG coherence per subject, red line shows mean across subjects. Shaded areas mark the frequency range represented in the source plots in panel A. Yellow locations on the inlayed cortical surface mark the corresponding location of the BA42 parcel on the source mesh. Code to reproduce source maps: `script_fig5.m`

4 Discussion

In the current study, we tested how frequency-specific oscillatory brain dynamics relate to expectation-based predictive processing in naturalistic language comprehension. We used well-defined information-theoretic metrics as an objective measure for how unexpected each heard word was given the past two words (word perplexity) and how predictable the upcoming input was (word entropy). Our approach allowed us to study brain dynamics in response to naturalistic, acoustically presented, linguistic signals. We observed predominantly left-lateralized effects, with low and high beta-band dynamics relating to fluctuations in perplexity and entropy, and theta-band dynamics to entropy modulations.

4.1 Beta-band dynamics reflect maintenance of context

Comparison of unexpected, high-perplexity words with expected, low-perplexity words showed that unexpected words were accompanied by lower neural source power in both the low and high beta-bands. Beta-band dynamics were also negatively related to stimulus entropy, that is, lower beta-band MEG source power was observed for high entropy (less predictive) contexts relative to low entropy (more predictive) context.

The beta effects reported are in line with the accounts proposing that decreases in beta-band power signal new processing demands in the neural system (Engel & Fries, 2010; Lewis & Bastiaansen, 2015; Weiss & Mueller, 2012). In the present study, a decrease in beta-band power upon encountering unexpected words possibly signals the need to revise and update the current representation of sentence and story contents. In contrast, if the words are less perplexing given the context, no substantial additional neural processing is needed to update the current contextual state, and beta-band dynamics are unperturbed. Similarly with entropy; in more predictable contexts, strong predictions are licensed which leads to sustained beta-band dynamics in higher-level areas, possibly providing input to areas involved in lexical or sensory processing.

The left-lateralized topology of perplexity-driven and entropy-driven beta-

band dynamics over central, temporal, and frontal areas supports its hypothesized general role of reflecting maintenance of contextual states of the system. Recent research has linked beta-band dynamics with sources in sensorimotor areas to the generation of temporal predictions to the auditory brain areas during auditory perception (Morillon & Baillet, 2017). Further, beta-band dynamics in left frontal areas have been found to modulate the strength of speech-brain coupling in auditory cortical areas during auditory story comprehension (Keitel, Ince, Gross, & Kayser, 2017). The exact computational role of (pre)motor and frontal areas in online speech perception and language comprehension remains an ongoing area of research (Lima, Krishnan, & Scott, 2016; Skipper, Devlin, & Lametti, 2017) and is beyond the focus of the present study. Suffice it to note presently that the topography of beta effects substantiates the interpretation that beta-band dynamics are involved in maintaining active states of the system, possibly for top-down predictions.

The observed left-lateralized beta-band dynamics are most prominent when the MEG signal is lagged relative to linguistic information for 600 msec, which reflects the fact that the computations of prediction (dis)confirmation or context-driven uncertainty cannot happen instantly, upon hearing the current word, but is rather only possible once the words that follow the current word have been observed. Given that average word duration in our stimuli was approximately between 200 and 300 milliseconds, a lag of 600 milliseconds seems a plausible latency at which contextual engagement and comparison of predictions based on the current context can be observed in brain signals.

It is interesting to note that perplexity-driven beta dynamics showed an earlier onset relative to entropy-driven beta. This is not unexpected, given the fact that computation of word perplexity depends crucially on the actually observed word, whereas word entropy, strictly speaking, is not the property of any word alone, but is instead a function of the distribution of *possible upcoming words* at the current word position in a sentence, a computation that likely requires longer latencies for it to be reflected in cortical signals. Our results on temporal progression of spectral modulations are in line with earlier reports

showing, among other, that lexical language model complexity metrics in general do not relate to early (peaking < 300 ms post word onset) language-related ERP components (Frank et al., 2015).

4.2 Theta dynamics relate to lexical uncertainty

In the current study, word entropy states are positively related to theta-band dynamics; that is, brain activity is higher in high entropy (less predictable) contexts. Entropy quantifies the uncertainty about the possible upcoming words at the currently heard word. Entropy is high if the two-word context up to the current word position can be completed by many possible words and low in cases when there are only a few, highly probable continuations.

From a psycholinguistic perspective, higher oscillatory activity for unpredictable continuations relative to predictable ones can be interpreted as support for accounts emphasizing that the amount of neural information-processing resources used increases with increased "competition" (i.e. increased entropy) between plausible continuations (see Marslen-Wilson, 1987, for such an account in auditory word recognition). The present results therefore do not corroborate—at least in terms of theta-band oscillatory activity—opposite accounts postulating that use of neural resources would increase with the amount of "predictive work" required, that is, in low entropy states when strong predictions are possible (see Ettinger, Linzen, & Marantz, 2014, for such an account and evidence in morphology). Theta-band dynamics, as reported here, then likely reflect input-driven lexical computations as opposed to predictive computations *per se*.

However, present patterns of results can also be accounted for in the framework of probabilistic inference (Chater & Manning, 2006; Kuperberg & Jaeger, 2016; Pouget et al., 2013) where it is postulated that the listener is constantly weighing the relevance of the incoming lexical evidence (currently processed word) and prior knowledge (here the minimal sentential context so far) for updating and inferring the model of the world (narrative contents).

In high-entropy situations, when the sentential context is not strongly predictive of upcoming words, the corresponding state of the relevant neural circuits

is less determined by their contextual history, but is instead more sensitive to the actually observed lexico-statistical properties of the incoming words (see Strange, Duggins, Penny, Dolan, & Friston, 2005, for a related interpretation of hippocampal modulations to stimulus entropy). Put differently, because the context affords only weak predictions, more information-processing work needs to be done on the currently observed words to foster evidence for inference and future efficient processing. Assuming that increases in theta-band MEG power reflect increased synchronous engagement of the underlying neuronal populations, the probabilistic processing account is corroborated by the fact that theta-band neural source power is higher in less vs. more predictive contexts.

Localization of the theta-band effects shows that these are strongly left-lateralized with a focal maximum in middle temporal areas, which adds credence to our interpretation that theta-band dynamics reflect increased sensitivity of neural systems to lexico-semantic evidence. In a recent meta-analysis, the left lateral temporal cortex has been suggested to be sensitive to lexico-semantic processing demands during sentence comprehension (Hagoort & Indefrey, 2014). In a recent MEG study, Lam, Schoffelen, Uddén, Hultén, and Hagoort (2016) source-localized word-related theta-band power decreases to left anterior temporal lobes. In addition, modulations in the theta-band have been consistently consistently linked to word-related computations in sentence processing tasks (M. Bastiaansen & Hagoort, 2015; M. C. Bastiaansen, Linden, Keurs, Dijkstra, & Hagoort, 2005; M. C. Bastiaansen, van Berkum, & Hagoort, 2002; Hald, Bastiaansen, & Hagoort, 2006; Kielar, Panamsky, Links, & Meltzer, 2015; Wang, Zhu, & Bastiaansen, 2012).

Alongside theta differences in the left lateral temporal cortical areas, we also observed prominent peaks in several medial cortical structures. Activation of these regions is well documented in fMRI studies of pragmatic text comprehension beyond single sentences (Ferstl, Neumann, Bogler, & von Cramon, 2008). In the memory literature, these areas are considered as core components of the extended posterior medial memory system (Ranganath & Ritchey, 2012) which is thought, among others, to underlie our ability to maintain the construction

of a mental representation of relations between entities denoted by the text, so-called situation models (Zwaan & Radvansky, 1998). Increased theta-band activity with high entropy could therefore be taken to signify increased use of neural resources for pragmatic and contextual computations in order to overcome high levels of lexical uncertainty induced by the text so far.

Finally, a potential concern could be that our spectral and spatial characteristics of entropy effects in fact coincide with the so-called acoustic entrainment effects which are typically observed in the theta frequency range over left and right superior temporal cortex (Lam et al., 2018). However, our MEG-audio coherence analysis indicates that the underlying neural sources have distinct spatial profiles with modest or no focal overlap; that is, entrainment due to acoustic properties of the input shows predominantly right-lateralized sources with peaks in the superior temporal areas as opposed to entropy-related effects which are predominantly left-lateralized with peaks in the middle temporal lobes. This suggest that entropy-related theta band dynamics reflect electrophysiological processes beyond responses to acoustic-sensory inputs alone.

4.3 Comparison with related prior work

To the best of our knowledge, only three other studies so far explored the relationship between probabilistic language complexity in electrophysiology (albeit using sentence reading task rather than auditory narrative comprehension). Frank et al. (2015) reported no significant relationship between next-word entropy and language-related ERPs in sentence reading after accounting for the effects of surprisal. In a recent ECoG study, Nelson, Karoui, et al. (2017) showed that bigram word entropy during sentence reading is negatively related with fluctuations in high gamma (70–150 Hz) power on electrodes surrounding left posterior temporal regions. In a separate analysis of the same dataset, Nelson, Dehaene, et al. (2017) showed that sentential entropy reduction (modeling per-word changes in grammatical uncertainty) was reported to have a positive linear relationship with high gamma power in the left anterior and posterior inferior temporal electrode sites.

There are several differences between the studies by Frank et al. (2015), Nelson, Karoui, et al. (2017) and our study, most notably the type and modality of stimuli used (visually presented sentences vs. auditory narratives) and recording modality (scalp recorded MEG and EEG vs. intracranial recordings). A possible explanation for the divergent findings with respect to the study by Frank et al. (2015) is that measuring neural responses in settings which more closely resemble those of the brain's natural mode of operation, brain dynamics will more readily reflect context-driven computations (captured by word entropy) which would explain why we find an effect of entropy in our dataset, but Frank et al. (2015) do not.

Second, different from Nelson, Karoui, et al. (2017), we do not observe significant modulations of high gamma power in response to changes in word entropy. A plausible reason is that high gamma responses can be more readily estimated in responses to visual stimulation as opposed to auditory stimulation where signal modulation is dominated by speech-induced low frequency power. Further, compared to ECoG signals, the signal-to-noise ratio of MEG, particularly in the frequency range reported by Nelson, Karoui, et al. (2017), as well as the more limited spatial resolution, may have prohibited accurate estimation of high frequency components in the current experiment.

4.4 Limitations and future work

Two limitations to our presently adopted approach deserve to be mentioned. First, we used lexical probabilistic language models defined over individual words whereas our brain responses were recorded during comprehension of connected discourse (narratives). One may wonder whether n-gram models of linguistic sequences are at all adequate for investigating naturalistic brain responses. Specifically, n-gram Markov models reduce context-dependent linguistic computation by requiring only the past $n-1$ words for generating expectation over upcoming words whereas it has been shown in the past that humans exploit much wider contextual cues rapidly in online comprehension (e.g. Nieuwland & Van Berkum, 2006).

It is beyond the scope of the present work to resolve the apparent discrepancy between the simplicity of statistical models embodying the Markov assumption and their success in engineering and psycholinguistic applications (see Jurafsky & Martin, 2009, for an overview). We are currently planning further experiments to test and compare models of linguistic sequences that capture richer contextual and temporal dimensions.

Second, in our investigation of the spectral characteristics of brain dynamics we relied on a relatively coarse binary complexity contrast (i.e. high vs. low complexity bins). However, our approach allows in principle for testing of parametric modulations in complexity and its relationship to brain responses using regression-based designs (e.g. as in Frank et al., 2015; Frank & Willems, 2017). Given the rather exploratory character of the present study, we opted for a simpler investigation of the relationship between frequency-specific MEG responses and complexity metrics.

We believe the current study provides ground for further research by evaluating models against brain oscillatory activity along other possible dimensions, for example type of information exploited by the model (e.g. lexical vs. non-lexical) or model architectures used (e.g. neural networks vs. symbolic architectures). In addition, especially interesting would be applications of recent multivariate techniques for extraction of the so-called "temporal response functions" (Crosse, Di Liberto, Bednar, & Lalor, 2016) from naturalistic MEG data on the basis of model-based predictors that embody distinct underlying hypotheses.

5 Conclusion

In the current study, we show that formalized probabilistic computations relate to frequency-specific brain dynamics during auditory narrative comprehension. We show that while theta-band dynamics relate to word-by-word contextual predictability likely reflecting lexical computations, beta-band dynamics are related both to word entropy and word perplexity, possibly reflecting maintenance of ongoing cognitive context which is updated upon encountering less expected words. Future challenges lie in using models that can exploit longer temporal

relationships between words in narratives and in estimating predictive computations over different levels of linguistic representation.

References

Ahissar, E., Nagarajan, S., Ahissar, M., Protopapas, A., Mahncke, H., & Merzenich, M. M. (2001, November). Speech comprehension is correlated with temporal response patterns recorded from auditory cortex. *Proceedings of the National Academy of Sciences*, *98*(23), 13367–13372. doi: 10.1073/pnas.201400998

Bach, D. R., & Dolan, R. J. (2012, August). Knowing how much you don't know: a neural organization of uncertainty estimates. *Nature Reviews Neuroscience*, *13*(8), 572–586. doi: 10.1038/nrn3289

Bar, M. (2009, May). Predictions: a universal principle in the operation of the human brain. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1521), 1181–1182. doi: 10.1098/rstb.2008.0321

Bastiaansen, M., & Hagoort, P. (2006, January). Oscillatory neuronal dynamics during language comprehension. In C. Neuper & W. Klimesch (Eds.), *Progress in Brain Research* (Vol. 159, pp. 179–196). Elsevier. doi: 10.1016/S0079-6123(06)59012-0

Bastiaansen, M., & Hagoort, P. (2015, November). Frequency-based segregation of syntactic and semantic unification during online sentence level language comprehension. *Journal of Cognitive Neuroscience*, *27*(11), 2095–2107. doi: 10.1162/jocn.a.00829

Bastiaansen, M. C., Linden, M. v. d., Keurs, M. t., Dijkstra, T., & Hagoort, P. (2005, March). Theta responses are involved in lexical—semantic retrieval during language processing. *Journal of Cognitive Neuroscience*, *17*(3), 530–541. doi: 10.1162/0898929053279469

Bastiaansen, M. C., van Berkum, J. J., & Hagoort, P. (2002, November). Syntactic processing modulates the theta Rhythm of the human EEG. *NeuroImage*, *17*(3), 1479–1492. doi: 10.1006/nimg.2002.1275

Bosch, A. v. d., Busser, B., Canisius, S., & Daelemans, W. (2007). An efficient memory-based morphosyntactic tagger and parser for Dutch. In P. Dirix (Ed.), *Computational Linguistics in the Netherlands 2006: Selected papers from the seventeenth CLIN Meeting* (pp. 191–206). Utrecht: LOT. Retrieved from http://www.cnts.ua.ac.be/papers/2007/tad07.pdf

Chater, N., & Manning, C. D. (2006, July). Probabilistic models of language processing and acquisition. *Trends in Cognitive Sciences*, *10*(7), 335–344. doi: 10.1016/j.tics.2006.05.006

Clark, A. (2013, June). Whatever next? Predictive brains, situated agents, and the future of cognitive science. *Behavioral and Brain Sciences*, *36*(03), 181–204. doi: 10.1017/S0140525X12000477

Crosse, M. J., Di Liberto, G. M., Bednar, A., & Lalor, E. C. (2016, November). The Multivariate temporal response function (mTRF) Toolbox: A MATLAB Toolbox for relating neural signals to continuous stimuli. *Frontiers in Human Neuroscience*, *10*, 604. doi: 10.3389/fnhum.2016.00604

den Ouden, H. E. M., Kok, P., & de Lange, F. P. (2012). How prediction errors shape perception, attention, and motivation. *Frontiers in Psychology*, *3*. doi: 10.3389/fpsyg.2012.00548

Engel, A. K., & Fries, P. (2010, April). Beta-band oscillations—signalling the status quo? *Current Opinion in Neurobiology*, *20*(2), 156–165. doi: 10.1016/j.conb.2010.02.015

Ettinger, A., Linzen, T., & Marantz, A. (2014, February). The role of morphology in phoneme prediction: Evidence from MEG. *Brain and Language*, *129*, 14–23. doi: 10.1016/j.bandl.2013.11.004

Ferstl, E. C., Neumann, J., Bogler, C., & von Cramon, D. Y. (2008, May). The extended language network: A meta-analysis of neuroimaging studies on text comprehension. *Human Brain Mapping*, *29*(5), 581–593. doi: 10.1002/hbm.20422

Frank, S. L., Otten, L. J., Galli, G., & Vigliocco, G. (2015, January). The ERP response to the amount of information conveyed by words in sentences. *Brain and Language*, *140*(Supplement C), 1–11. doi: 10.1016/j.bandl.2014

.10.006

Frank, S. L., & Willems, R. M. (2017, October). Word predictability and semantic similarity show distinct patterns of brain activity during language comprehension. *Language, Cognition and Neuroscience*, *32*(9), 1192–1203. doi: 10.1080/23273798.2017.1323109

Friston, K. (2005, April). A theory of cortical responses. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *360*(1456), 815–836. doi: 10.1098/rstb.2005.1622

Giordano, B. L., Ince, R. A. A., Gross, J., Schyns, P. G., Panzeri, S., & Kayser, C. (2017, June). Contributions of local speech encoding and functional connectivity to audio-visual speech perception. *eLife*, *6*. doi: 10.7554/eLife.24763

Gross, J., Hoogenboom, N., Thut, G., Schyns, P., Panzeri, S., Belin, P., & Garrod, S. (2013, December). Speech rhythms and multiplexed oscillatory sensory coding in the human brain. *PLoS Biology*, *11*(12), e1001752. doi: 10.1371/journal.pbio.1001752

Gross, J., Kujala, J., Hamalainen, M., Timmermann, L., Schnitzler, A., & Salmelin, R. (2001, January). Dynamic imaging of coherent sources: Studying neural interactions in the human brain. *Proceedings of the National Academy of Sciences*, *98*(2), 694–9. doi: 10.1073/pnas.98.2.694

Hagoort, P., & Indefrey, P. (2014, July). The neurobiology of language beyond single words. *Annual Review of Neuroscience*, *37*(1), 347–362. doi: 10.1146/annurev-neuro-071013-013847

Hald, L. A., Bastiaansen, M. C., & Hagoort, P. (2006, January). EEG theta and gamma responses to semantic violations in online sentence processing. *Brain and Language*, *96*(1), 90–105. doi: 10.1016/j.bandl.2005.06.007

Hale, J. (2016, September). Information-theoretical complexity metrics. *Language and Linguistics Compass*, *10*(9), 397–412. doi: 10.1111/lnc3.12196

Hasson, U. (2017, January). The neurobiology of uncertainty: implications for statistical learning. *Phil. Trans. R. Soc. B*, *372*(1711), 20160048. doi: 10.1098/rstb.2016.0048

Henderson, J. M., Choi, W., Lowder, M. W., & Ferreira, F. (2016, May). Language structure in the brain: A fixation-related fMRI study of syntactic surprisal in reading. *NeuroImage*, *132*(Supplement C), 293–300. doi: 10.1016/j.neuroimage.2016.02.050

Huettig, F., & Mani, N. (2016, January). Is prediction necessary to understand language? Probably not. *Language, Cognition and Neuroscience*, *31*(1), 19–31. doi: 10.1080/23273798.2015.1072223

Jenkinson, M., Beckmann, C. F., Behrens, T. E., Woolrich, M. W., & Smith, S. M. (2012, August). FSL. *NeuroImage*, *62*(2), 782–790. doi: 10.1016/j.neuroimage.2011.09.015

Jurafsky, D., & Martin, J. H. (2009). *Speech and language processing: an introduction to natural language processing, computational linguistics, and speech recognition* (2nd ed ed.). Upper Saddle River, N.J: Pearson Prentice Hall. (OCLC: 213375806)

Keitel, A., Ince, R. A., Gross, J., & Kayser, C. (2017, February). Auditory cortical delta-entrainment interacts with oscillatory power in multiple fronto-parietal networks. *NeuroImage*, *147*, 32–42. doi: 10.1016/j.neuroimage.2016.11.062

Keuleers, E., Brysbaert, M., & New, B. (2010, August). SUBTLEX-NL: A new measure for Dutch word frequency based on film subtitles. *Behavior Research Methods*, *42*(3), 643–650. doi: 10.3758/BRM.42.3.643

Kielar, A., Panamsky, L., Links, K. A., & Meltzer, J. A. (2015, January). Localization of electrophysiological responses to semantic and syntactic anomalies in language comprehension with MEG. *NeuroImage*, *105*, 507–524. doi: 10.1016/j.neuroimage.2014.11.016

Kuperberg, G. R., & Jaeger, T. F. (2016, January). What do we mean by prediction in language comprehension? *Language, Cognition and Neuroscience*, *31*(1), 32–59. doi: 10.1080/23273798.2015.1102299

Lam, N. H. L., Hultén, A., Hagoort, P., & Schoffelen, J.-M. (2018, February). Robust neuronal oscillatory entrainment to speech displays individual variation in lateralisation. *Language, Cognition and Neuro-*

science, *0*(0), 1–12. Retrieved 2018-03-09, from https://doi.org/10.1080/23273798.2018.1437456 doi: 10.1080/23273798.2018.1437456

Lam, N. H. L., Schoffelen, J.-M., Uddén, J., Hultén, A., & Hagoort, P. (2016, November). Neural activity during sentence processing as reflected in theta, alpha, beta, and gamma oscillations. *NeuroImage*, *142*, 43–54. Retrieved 2018-03-13, from http://www.sciencedirect.com/science/article/pii/S1053811916002032 doi: 10.1016/j.neuroimage.2016.03.007

Lewis, A. G., & Bastiaansen, M. (2015, July). A predictive coding framework for rapid neural dynamics during sentence-level language comprehension. *Cortex*, *68*, 155–168. doi: 10.1016/j.cortex.2015.02.014

Lima, C. F., Krishnan, S., & Scott, S. K. (2016, August). Roles of supplementary motor areas in auditory processing and auditory imagery. *Trends in Neurosciences*, *39*(8), 527–542. doi: 10.1016/j.tins.2016.06.003

Lopopolo, A., Frank, S. L., van den Bosch, A., & Willems, R. M. (2017, May). Using stochastic language models (SLM) to map lexical, syntactic, and phonological information processing in the brain. *PLOS ONE*, *12*(5), e0177794. Retrieved 2018-02-05, from http://dx.plos.org/10.1371/journal.pone.0177794 doi: 10.1371/journal.pone.0177794

Luo, H., & Poeppel, D. (2007, June). Phase patterns of neuronal responses reliably discriminate speech in human auditory cortex. *Neuron*, *54*(6), 1001–1010. Retrieved 2018-03-07, from http://linkinghub.elsevier.com/retrieve/pii/S0896627307004138 doi: 10.1016/j.neuron.2007.06.004

Maris, E., & Oostenveld, R. (2007, August). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*, *164*(1), 177–190. doi: 10.1016/j.jneumeth.2007.03.024

Marslen-Wilson, W. D. (1987, March). Functional parallelism in spoken word-recognition. *Cognition*, *25*(1-2), 71–102. doi: 10.1016/0010-0277(87)90005-9

Morillon, B., & Baillet, S. (2017, October). Motor origin of temporal predictions in auditory attention. *Proceedings of the National Academy of Sciences*, *114*(42), E8913–E8921. Retrieved 2018-06-11, from http://www.pnas.org/

lookup/doi/10.1073/pnas.1705373114 doi: 10.1073/pnas.1705373114

Nelson, M. J., Dehaene, S., Pallier, C., & Hale, J. T. (2017, April). Entropy reduction correlates with temporal lobe activity. In *Proceedings of the 7th Workshop on Cognitive Modeling and Computational Linguistics* (pp. 1–10). Valencia, Spain: Association for Computational Linguistics.

Nelson, M. J., Karoui, I. E., Giber, K., Yang, X., Cohen, L., Koopman, H., ... Dehaene, S. (2017, May). Neurophysiological dynamics of phrase-structure building during sentence processing. *Proceedings of the National Academy of Sciences*, *114*(18), E3669–E3678. Retrieved 2017-11-22, from http://www.pnas.org/content/114/18/E3669 doi: 10.1073/pnas.1701590114

Nieuwland, M. S., & Van Berkum, J. J. A. (2006, July). When peanuts fall in love: N400 evidence for the power of discourse. *Journal of Cognitive Neuroscience*, *18*(7), 1098–1111. doi: 10.1162/jocn.2006.18.7.1098

Nolte, G. (2003, November). The magnetic lead field theorem in the quasi-static approximation and its use for magnetoencephalography forward calculation in realistic volume conductors. *Physics in Medicine and Biology*, *48*(22), 3637–3652. doi: 10.1088/0031-9155/48/22/002

Oostdijk, N. (2000). The Spoken Dutch Corpus: Overview and first evaluation. In *Proceedings of Second International Conference on Language Resources and Evaluation (LREC)* (pp. 887–894).

Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open Source Software for Advanced Analysis of MEG, EEG, and Invasive Electrophysiological Data. *Computational Intelligence and Neuroscience*. doi: 10.1155/2011/156869

Park, H., Ince, R., Schyns, P., Thut, G., & Gross, J. (2015, June). Frontal top-down signals increase coupling of auditory low-frequency oscillations to continuous speech in human listeners. *Current Biology*, *25*(12), 1649–1653. doi: 10.1016/j.cub.2015.04.049

Pouget, A., Beck, J. M., Ma, W. J., & Latham, P. E. (2013, September). Probabilistic brains: knowns and unknowns. *Nature Neuroscience*, *16*(9), 1170–1178. doi: 10.1038/nn.3495

Ranganath, C., & Ritchey, M. (2012, October). Two cortical systems for memory-guided behaviour. *Nature Reviews Neuroscience*, *13*(10), 713–726. doi: 10.1038/nrn3338

Schäfer, R., & Bildhauer, F. (2012). Building large corpora from the web using a new efficient tool chain. In *Proceedings of the Eighth International Conference on Language Resources and Evaluation (LREC'12)* (pp. 486–493). European Language Resources Association (ELRA). Retrieved from http://dblp.uni-trier.de/db/conf/lrec/lrec2012.html#SchaferB12

Skipper, J. I., Devlin, J. T., & Lametti, D. R. (2017, January). The hearing ear is always found close to the speaking tongue: Review of the role of the motor system in speech perception. *Brain and Language*, *164*, 77–105. doi: 10.1016/j.bandl.2016.10.004

Smith, S. M. (2002, November). Fast robust automated brain extraction. *Human Brain Mapping*, *17*(3), 143–155. Retrieved 2017-12-14, from http://doi.wiley.com/10.1002/hbm.10062 doi: 10.1002/hbm.10062

Smith, Z. M., Delgutte, B., & Oxenham, A. J. (2002, March). Chimaeric sounds reveal dichotomies in auditory perception. *Nature*, *416*(6876), 87–90. Retrieved 2017-12-14, from http://www.nature.com/articles/416087a doi: 10.1038/416087a

Stolcke, A. (2002, September). SRILM - an Extensible Language Modeling Toolkit. In *ICSLP-2002* (pp. 901–904). Denver, Colorado, USA. Retrieved from http://www.isca-speech.org/archive/icslp.2002/i02.0901.html

Stolk, A., Todorovic, A., Schoffelen, J.-M., & Oostenveld, R. (2013, March). Online and offline tools for head movement compensation in MEG. *NeuroImage*, *68*(Supplement C), 39–48. Retrieved 2017-12-14, from http://www.sciencedirect.com/science/article/pii/S1053811912011597 doi: 10.1016/j.neuroimage.2012.11.047

Strange, B. A., Duggins, A., Penny, W., Dolan, R. J., & Friston, K. J. (2005, April). Information theory, novelty and hippocampal responses: unpredicted or unpredictable? *Neural Networks*, *18*(3), 225–230. doi: 10.1016/j.neunet.2004.12.004

van den Bosch, A., & Berck, P. (2009, January). Memory-based machine translation and language modeling. *The Prague Bulletin of Mathematical Linguistics*, *91*(-1). doi: 10.2478/v10108-009-0012-8

Veen, B. D. V., Drongelen, W. V., Yuchtman, M., & Suzuki, A. (1997, September). Localization of brain electrical activity via linearly constrained minimum variance spatial filtering. *IEEE Transactions on Biomedical Engineering*, *44*(9), 867–880. doi: 10.1109/10.623056

Wang, L., Zhu, Z., & Bastiaansen, M. (2012). Integration or predictability? A further specification of the functional role of gamma oscillations in language comprehension. *Frontiers in Psychology*, *3*. doi: 10.3389/fpsyg.2012.00187

Weiss, S., & Mueller, H. M. (2012). "Too many betas do not spoil the broth": the role of beta brain oscillations in language processing. *Frontiers in Psychology*, *3*. doi: 10.3389/fpsyg.2012.00201

Willems, R. M., Frank, S. L., Nijhof, A. D., Hagoort, P., & van den Bosch, A. (2016, June). Prediction during natural language comprehension. *Cerebral Cortex*, *26*(6), 2506–2516. doi: 10.1093/cercor/bhv075

Willems, R. M., Haegen, L. V. d., Fisher, S. E., & Francks, C. (2014, March). On the other hand: including left-handers in cognitive neuroscience and neurogenetics. *Nature Reviews Neuroscience*, *15*(3), 193. Retrieved 2017-12-14, from https://www.nature.com/articles/nrn3679 doi: 10.1038/nrn3679

Zwaan, R. A., & Radvansky, G. A. (1998). Situation models in language comprehension and memory. *Psychological Bulletin*, *123*(2), 162–185. doi: 10.1037/0033-2909.123.2.162

A Questionnaire

870

fn001078
Met welk voertuig komt de verteller aan?
a) Een boot
b) Een vliegtuig
c) Per trein
Answer: b)

Aan welke rivier ligt de stad waar hij aan komt?
a) De Amazone
b) De Mississippi
c) De Rijn
Answer: a)

fn001155
In welk landschap bevindt de hoofdpersoon zich?
a) De jungle
b) Rivierdelta
c) Woestijn
Answer: c)

Wat voor een natuurramp heeft plaatsgevonden?
a) Een orkaan
b) Een aardbeving
c) Een tsunami
Answer: b)

fn001293
Welke dieren ziet de hoofdpersoon aan de bosrand?
a) Herten
b) Elanden
c) Wolven
Answer: a)

Hoe is het weer in het verhaal?
a) Zeer warm
b) Koud
c) Wordt niet beschreven
Answer: b)

fn001443
Waar bevindt de hoofdpersoon zich?

a) In de bergen
b) In de woestijn
c) Op een eiland

Answer: c)

Hoe heet de afwezige vriend van de hoofdpersoon?

a) Harald
b) Jonathan
c) Simon

Answer: b)

fn001498

Welk dier brengt ongeluk volgens het verhaal?

a) Raaf
b) Vleermuis
c) Uil

Answer: c)

Waar is een van de personages mee gestopt?

a) Roken
b) Drinken
c) Gokken

Answer: a)