Structure and meaning organize neural oscillations into a content-specific hierarchy

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Abstract

Neural oscillations track acoustic and linguistic components during speech comprehension (e.g., Ding et al., 2016; Keitel et al., 2018). While previous research has shown that oscillatory activity is modulated by acoustic landmarks and intelligibility (e.g., Zoefel & VanRullen, 2015), it is unclear which information the brain utilizes to generate higher-level linguistic structure and meaning. This study uses electroencephalography (EEG) to investigate whether neural oscillatory responses are modulated by linguistic representation over and above that information's distribution at different timescales (i.e., contrasting content with timescale) and over and above acoustically matched controls. EEG was recorded while 29 male and female adult native speakers listened to naturally spoken Dutch sentences, jabberwocky items with sentence-like prosody and morphology, and word lists, designed to contrast acoustic-prosodic and lexical-semantic information in the signal. This allowed us to manipulate the amount of semantically and syntactically deployable information in spoken utterances apart from timescale. Mutual information (MI) analysis revealed enhanced speech tracking for content at distinct timescales: Phase MI was highest at the phrasal timescale (0.8-1.1 Hz) for sentences, suggesting that delta-band tracking is modulated by lexically-driven syntactic processing. At the word timescale (1.9-2.8 Hz), phase MI was higher for sentences than for jabberwocky items, suggesting that linguistic information modulates the oscillatory phase response at distinct timescales. Our findings indicate that neural tracking is enhanced for linguistic structures at timescales specific to that structure's role in the unfolding meaning of the sentence, consistent with neurophysiologically inspired models of language comprehension (Martin, 2016; Martin & Doumas, 2017).

Keywords: sentence comprehension, prosody, lexical semantics, combinatorial processing, mutual information, EEG, neural oscillations

Significance Statement

Biological systems like the brain encode their environment not only by reacting in a series of stimulus-driven responses, but by combining stimulus-driven information with internally generated, inferential knowledge and meaning. Understanding language from speech is the human benchmark for this. Much research focusses on the purely stimulus-driven response, but here, we focus on the goal of language behavior: conveying structure and meaning. To that end, we use naturalistic stimuli that contrast acoustic-prosodic and lexical-semantic information to show that, during spoken language comprehension, oscillatory modulations reflect computations related to inferring structure and meaning from the acoustic signal. Our experiment provides the first evidence to date that compositional structure and meaning organize the oscillatory response, above and beyond acoustic and lexical controls.

Introduction

Language is a critical biological signal for humans. From either speech or sign, the brain must convert sensory correlates into abstract, structured meanings. In the case of speech, the biological signal is, in its physical essence, a series of quasi-periodic fluctuations of air pressure. How the brain maps the acoustics of speech onto abstract structure and meaning remains a core question across cognitive science and neuroscience. A large body of research has shown that neural populations closely align their phase ("entrain") to the envelope of the speech signal, which correlates with the syllable rate (see, e.g., Peelle & Davis, 2012; Zoefel & VanRullen, 2015 for comprehensive reviews). In fact, information conveyed at the syllable frequency constitutes the acoustically most prominent timescale in the signal (Ding et al., 2018). Yet, while the syllable frequency is undoubtedly of crucial importance for speech perception (e.g., Kösem et al., 2018), the behavioral "goal" of speech and language

processing is the transmission of higher-level compositional structure and meaning, which are not simple correlates of the acoustic signal. However, the degree to which the neural response encodes higher-level linguistic information beyond the syllable level is relatively poorly understood, and computational or mechanistic models that make clear predictions at the interface between speech processing and language processing beyond the syllable envelope are sparse (cf. Alday, 2019). In this study, we show that neural responses to linguistic structures are enhanced for the most structured and meaningful representations that are available at a given timescale. As such, our experiment offers novel insights into how biological systems like the brain encode their environment; not only by reacting in a series of stimulus-driven responses, but by combining stimulus-driven information with internally generated, inferential knowledge and meaning.

Cortical entrainment has been defined as the process of endogenous neuronal populations aligning their phase to that of an exogenous stimulus (e.g., Schroeder & Lakatos, 2009; see Obleser & Kayser, 2019, for an excellent discussion of the use of the term "entrainment"). Consequently, entrainment in frequency bands beyond the syllable envelope (i.e., the delta band) has been hypothesized to reflect a chunking mechanism, dividing the signal into prosodic phrases based on acoustic cues (e.g., Bonhage, Meyer, Gruber, Friederici, & Mueller, 2017; Ghitza, 2017). Crucially, however, delta-band oscillations have also been linked to the top-down generation of hierarchically structured representations, such as phrases, clauses and sentences (e.g., Ding et al., 2017; Ding, Melloni, Zhang, Tian, & Poeppel, 2016; Meyer, Henry, Gaston, Schmuck, & Friederici, 2016). These higher-level linguistic units do not exhibit a diagnostic physical manifestation in the acoustic signal in a straight-forward manner.[1]

[1] That is, even though phrases, clauses, and sentences can at times be cued by acoustic-prosodic means (e.g., silent pauses, filled pauses, final lengthening, fundamental frequency reset, etc.; cf. Bosker, Pinget, Quené, Sanders, & De Jong 2013), they are less easily detectable in the acoustic signal compared to

Consequently, if one commits to a strictly physiological view where entrainment is, by definition, a response to rhythmic regularities of an *extrinsic* stimulus, it is unclear what the brain "entrains" to. We believe it is highly unlikely that an intrinsic "sentence" or "phrase oscillator" exists, other than as an emergent behavior of groups of neuronal assemblies processing in synchrony during sentence comprehension. Instead, we argue that phase alignment (or "entrainment in the broad sense", as defined by Obleser & Kayser, 2019) of neuronal populations to linguistic units that do *not* have straight-forward physically diagnostic representations in the acoustic signal (such as phrases, clauses and sentences) may reflect a process of perceptual inference (Martin, 2016). This would be in line with linguistic models of cue integration (Martin, 2016; Martin & Doumas, 2017), which posit that abstract linguistic representations are inferred from the acoustic signal through iterative summation and normalization of sensory cues. For clarity, we will use the term "tracking" throughout this paper to indicate the phase alignment of brain responses to both external, stimulus-driven information (e.g., the amplitude envelope of the speech signal) *and* internal, inferred information (e.g., linguistic units such as words, phrases and sentences).

Results reported by Ding et al. (2016, 2017) yielded promising evidence that cortical networks may, indeed, reflect tracking of intrinsically generated syntactic structures beyond the syllable envelope. Ding and colleagues showed that, when presented with a stream of synthesized isochronous syllables that could be combined into phrases and sentences, M/EEG responses reflected oscillatory activity not only at the syllable frequency, but also at the frequencies of phrases and sentences. Since the acoustic stimuli were synthesized and manipulated in such a way that they did not carry any prosodic or acoustic cues beyond the syllable rhythm, the phrase- and sentence-

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syllables (which are obvious from a clear peak in the modulation spectrum of speech; Ding et al., 2014, 2016).

level oscillatory activity is likely to reflect cortical tracking of intrinsically generated linguistic structures. However, despite this elegant design, the removal of the natural distribution of information in co-articulation and prosody somewhat limits the conclusions that can be drawn about how higher-level linguistic structures are computed from natural speech. In a similar vein, Keitel, Gross & Kayser (2018) showed that the brain closely tracks the speech signal in frequency bands corresponding to the occurrence rate of phrases, words, syllables and phonemes in natural speech (audiobooks). This tracking was significantly stronger for intelligible speech than for reversed stimuli and enhanced for correctly as opposed to incorrectly comprehended stimuli, again suggesting that measures of neuronal tracking are sensitive to the frequency of abstract linguistic units (Keitel et al., 2018; see also Gross et al., 2013). However, the experiments reported by Ding et al. (2016, 2017), Gross et al. (2013) and Keitel et al. (2018) could not discriminate between cortical responses being driven by the *timing* or *frequency* of these linguistic structures, or by the *informational content of the structure itself* (cf. Frank & Yang, 2018). We view this distinction as crucial: does the brain track inferred higher-level units such as phrases and words because they can be inferred at a given frequency, or does it attune to whether these units are structurally and semantically meaningful? If the latter, then it follows that oscillatory modulations reflect computations across populations of neurons involved in representing structure and meaning.

As a first step in understanding how listeners infer information that is not physically encoded in a straight-forward manner in the acoustics and temporal structure of natural speech, we ask if the neural response to syllables, words and phrases selectively attunes to stimuli as a function of our knowledge of language, and not just as a function of the timescales that information occurs on. In other words, is neural

tracking of natural speech driven by structure and meaning beyond acoustic-prosodic modulations and lexical, non-compositional semantics? To this end, we use a variety of controls to assess the degree to which different types of linguistic information drive phase alignment. The core control of our experimental design is backwards speech, which has an identical modulation spectrum for each forward condition. The three forward conditions, Sentences, prosodic-control Jabberwocky, and lexical-semantics-control Wordlist, were constructed in order to contrast two core sources of linguistic representations during speech and language processing: prosodic structure, which can, but does not always, correlate with syntactic and information structure, and lexical semantics, which arises in isolated words and concepts. Participants listened to naturally spoken, structurally homogenous sentences, jabberwocky items, and word lists (see Table 1 for an example from each condition). Using electroencephalography (EEG), we analyzed phase tracking of units at linguistically relevant timescales as quantified by Mutual Information (MI) – a typical measure of neural tracking that captures the informational similarity between two signals (Gross et al., 2013; Kayser, Ince, Gross, & Kayser, 2015; Keitel et al., 2018; Keitel, Ince, Gross, & Kayser, 2017). Figure 1 shows an overview of the experimental design and analysis pipeline.

To summarize, Ding et al. (2016, 2017) used synthesized, isochronous stimuli that allowed them to elegantly test their hypotheses, but at the same time limited the conclusions that could be drawn about naturalistic spoken language processing. Keitel et al. (2018) used naturalistic stimuli, but like Ding and colleagues, they could not analyze the specific contribution of linguistic structure and meaning in distinct timescales. As such, our experiment goes beyond the existing literature and offers novel insights into how linguistic structure and meaning influence the neural response *above and beyond* the timescales at which that information occurs. In short, we try to tease

apart the way that content and timescales shape the response, which our experimental design disentangles through our condition manipulation.

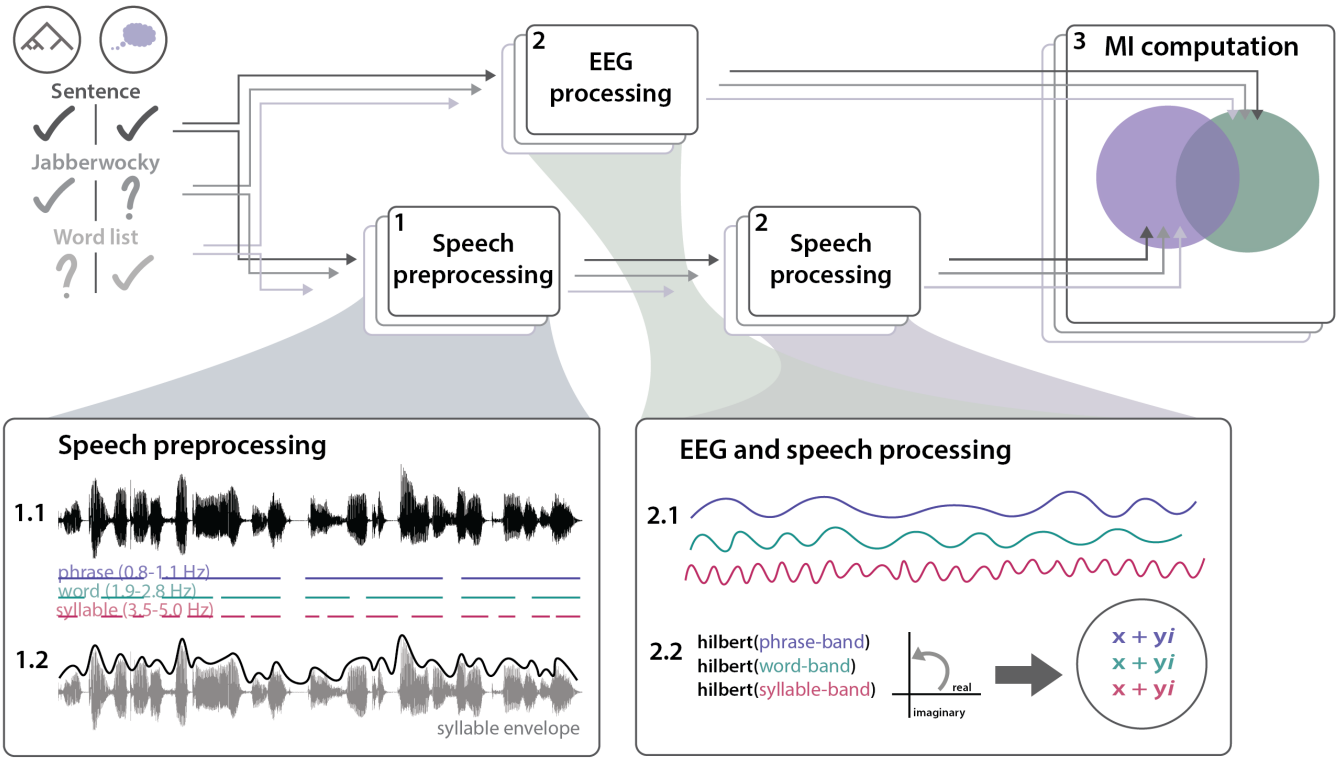

Figure 1. Experimental design and analysis pipeline. Participants listened to sentences, jabberwocky items, and word lists while their brain response was recorded using EEG. Step 1: Speech Processing. 1.1) The speech signal is annotated for the occurrence of phrases, words, and syllables in the stimuli. Based on this, frequency bands of interest for each of the linguistic units can be identified. 1.2) A cochlear filter is applied to the speech stimuli and the amplitude envelope is extracted. Step 2: Further processing is identical for both speech and EEG modalities. 2.1) Broadband filters are applied in the previously identified frequency bands of interest. 2.2) Hilbert transforms are computed in each filtered signal, and real and imaginary parts of the Hilbert transform output are used for further analysis. Step 3: MI Computation. Mutual information is computed between the pre-processed speech and EEG signal in each of the three conditions and their respective backward controls.

Materials and Methods

Participants

35 native Dutch speakers (9 males; age range 19-32; mean age=23) participated in the experiment. They were recruited from the Max Planck Institute for Psycholinguistics' participant database with written consent approved by the Ethics Committee of the Social Sciences Department of Radboud University (Project code: ECSW2014-1003-196a). All participants in the experiment reported normal hearing and were remunerated for their participation.

Materials

The experiment used three critical conditions: Sentence, Jabberwocky, and Wordlist. Eighty sets (triplets) of the three conditions (Sentence, Jabberwocky, Wordlist) were created, resulting in 240 stimuli. In addition to one "standard" forward presentation of each stimulus, participants also listened to a version of each of the stimuli played backwards, thus resulting in a total of 480 stimuli.

Dutch stimuli consisted of 10 words, which were all disyllabic except for "de" (*the*) and "en" (*and*), thus resulting in 18 syllables in total. Sentences all consisted of two coordinate clauses, which followed the structure *[Adj N V N Conj Det Adj N V N]*. Word lists consisted of the same 10 words as in the Sentence condition, but scrambled in syntactically implausible ways (either *[V V Adj Adj Det Conj N N N N],* or *[N N N N Det Conj V V Adj Adj]*, in order to avoid any plausible internal combinations of words). Jabberwocky items were created using the wuggy pseudoword generator (Keuleers & Brysbaert, 2010), following the same syntactic structure as the Sentences. Table 1 shows an example of stimuli in each condition.

Table 1. Example items in Sentence, Jabberwocky, and Wordlist conditions. Sentences consisted of 10 words (disyllabic, except for "de" (*"the")* and "en" (*"and"*)) and carried sentence prosody. Jabberwocky items consisted of 10 pseudo-words with morphology; they also carried sentence prosody. Word lists consisted of the same 10 words as the Sentence condition, but scrambled so as to be syntactically implausible. They had list-prosody. Marked with square brackets are "phrases" in all three conditions.

Sentence	**Jabberwocky**	**Wordlist**
[Bange helden] [plukken bloemen] en de [bruine vogels] [halen takken].	[Garge ralden] [spunken] [drijmen] en de [druize gomels] [paven mukken].	[helden bloemen] [vogels takken] de en [plukken halen] [bange bruine]
[Timid heroes] [pluck flowers] and the [brown birds] [gather branches].	*[Flimid lerops] [bruck clowters] and the [trown plirds] [shmather blamches].*	*[heroes flowers] [birds branches] the and [pluck gather] [timid brown]*

Forward stimuli were recorded by a female native speaker of Dutch in a sound-attenuating recording booth. All stimuli were recorded at a sampling rate of 44100 Hz (mono), using the Audacity sound recording and analysis software (Audacity Team,

2014). After recording, pauses were normalized to ~150 ms in all stimuli, and the intensity was scaled to 70 dB using the Praat voice analysis software (Boersma & Weenink, 2017). Stimuli from all three conditions were then reversed using Praat. Figure 3 shows modulation spectra for forward and backward conditions. Please see the Appendix for pilot data confirming participants' perception of the linguistic content of each condition.

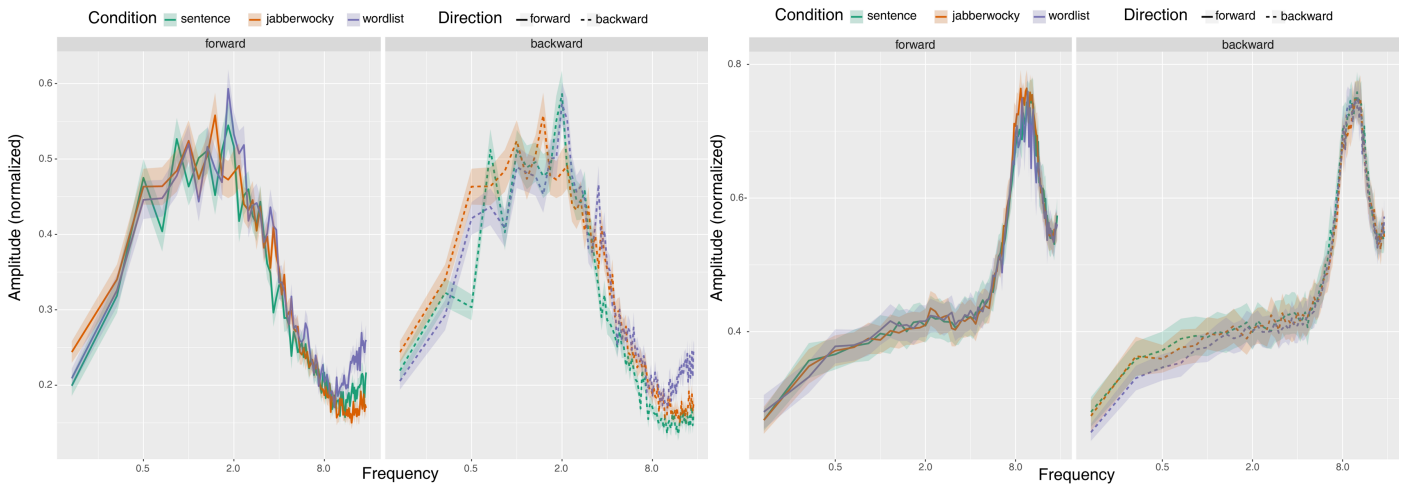

Figure 2. Modulation Spectra of forward and backward stimuli. Green: Sentences; Orange: Jabberwocky; Purple: Wordlist. Modulation spectra were calculated following the procedure and Matlab script described in Ding et al. (2017). Note that small deviations between the modulation spectrum of each forward condition and its backward counterpart are due to numerical inaccuracy; mathematically, the frequency components of forward and backward stimuli are identical.

Procedure

Participants were tested individually in a sound-conditioned and Faraday-cage enclosed booth. They first completed a practice session with 4 trials (one from each forward condition and one backward example) to become familiarized with the task. All 80 stimuli from each condition were presented to the participants in separate blocks. The order of the blocks was pseudorandomized across listeners, and the order of the items within each block was randomized. During each trial, participants were instructed to look at a fixation cross which was displayed at the center of the screen (to minimize eye movements during the trial), and listen to the audio, which was presented to them at a comfortable level of loudness. After each trial, participants could advance to the next

item via a button-press. After each block, participants were allowed to take a self-paced break. The experiment was run using the Presentation software (Neurobehavioral Systems) and took about 50-60 minutes to complete. EEG was continuously recorded with a 64-channel EEG system (MPI equidistant montage) using BrainVision Recorder™ software, digitized at a sampling rate of 500 Hz and referenced to the left mastoid. The impedance of electrodes was kept below 25 kO. Data was re-referenced offline to the electrode average.

EEG Data Preprocessing

The analysis steps were carried out using the FieldTrip analysis toolkit revision 20180320 (Oostenveld, Fries, Maris, & Schoeffelen, 2011) on MATLAB version 2016a (MathWorks, Inc.). Six participants were excluded from the analysis due to excessive artifact contamination. The raw EEG signal was segmented into a series of variable length epochs, starting at 200 ms before the onset of the utterance and lasting until 200 ms after its end. The signal was low-pass filtered to 70 Hz, and a 50-Hz bandpass filter was applied in each epoch to exclude line noise (both zero-phase FIR filters using Hamming windows). Channels contaminated with excessive noise were excluded from the analysis. Independent component analysis was performed on the remaining channels, and components related to eye movements, blinking, or motion artifacts, were subtracted from the signal. Epochs containing voltage fluctuations exceeding ±100 μV or transients exceeding ±75 μV were excluded from further analysis. We selected a cluster of 22 electrodes for all further analyses based on previous studies that found broadly-distributed effects related to sentence processing (e.g., Kutas, Van Petten & Kluender, 2006; Kutas & Federmeier, 2000; see also Ding et al., 2017). Specifically, the electrode selection included the following electrodes: 1, 2, 3, 4, 5, 8, 9, 10, 11, 28, 29,

30, 31, 33, 34, 35, 36, 37, 40, 41, 42, 43 (electrode names based on the MPI equidistant layout).

Speech Preprocessing

For each stimulus, we computed the wideband speech envelope at a sampling rate of 150 Hz following the procedure reported by Keitel et al. (2018) and others (e.g., Bosker & Cooke, 2018; Gross et al., 2013; Keitel et al., 2017). We first filtered the acoustic waveforms into 8 frequency bands (100-8,000 Hz; third-order Butterworth filter, forward and reverse), equidistant on the cochlear frequency map (Smith, Delgutte, & Oxenham, 2002). We then estimated the wideband speech envelope by computing the magnitude of the Hilbert transformed signal in each band and averaging across bands.

The timescales of interest for further Mutual Information analysis were identified in a similar fashion as described in Keitel et al. (2018). We first annotated the occurrence of linguistic units (phrases, words, and syllables) in the speech stimuli. Here, phrases were defined as noun-adjective-verb combinations (e.g., in the Sentence condition: "bange helden" – *timid heroes*; "plukken bloemen" – *pluck flowers,* and so on.*;* in the Jabberwocky condition: "garge ralden" – *flimid lerops* etc.; in the Wordlist condition, a "pseudo-phrase" corresponds to adjacent noun-noun, verb-verb and adjective-adjective pairs, e.g., "helden bloemen" – *heroes flowers*). Unit-specific bands of interest were then identified by converting each of the rates into frequency ranges across conditions. This resulted in the following bands: 0.8-1.1 Hz (phrases); 1.9-2.8 Hz (words); and 3.5-5.0 Hz (syllables).[2]

[2] Note that the problem the brain faces during spoken language comprehension is even more complex than this, because the timescales of linguistic units can highly overlap, even within a single sentence. Oscillators that "entrain" to words will thus also have to be sensitive to information that occurs outside of these – rather narrow – frequency bands. We also computed MI values within wider frequency bands that were based on the absolute minimum and maximum duration of units at each timescale across all stimuli

For the exploratory annotation-based MI analysis (section Results, subsection *Tracking of abstract linguistic units*), we further created linguistically abstracted versions of our stimuli. Specifically, our aim was to create annotations that captured linguistic information at the phrase frequency *independent of* the acoustic signal. Based on the word-level annotations of our stimuli, we created dimensionality-reduced arrays for further analysis, similar to the "Semantic composition" analyses reported by Brodbeck et al. (2019). Specifically, we identified all time points in the spoken materials where words could be integrated into phrases, and marked each of these words associated with phrase composition (e.g., in a sentence such as "bange helden plukten bloemen en de bruine vogels halen takken" (*timid heroes pluck flowers and the brown birds gather branches*), the words "helden" (*heroes*), "bloemen" (*flowers*), "vogels" (*birds*) and "takken" (*branches*) were marked). All these critical words were coded as 1 for their entire duration, while all other timepoints (samples) were marked as 0 (cf. Brodbeck et al., 2019). This resulted in an abstract "spike train" array of phrase-level structure building that is independent of the acoustic envelope. We repeated this procedure for all items individually in all three conditions, since our stimuli were naturally spoken and thus differed slightly in duration and time course. Note that, consequently, this "phrase-level composition array" is somewhat arbitrary for the Wordlist condition as there are, per definition, no phrases in a word list. We annotated "pseudo-phrases" the same way as shown in Table 1. The procedure is visualized in Figure 3.

(phrases: 0.6-1.5 Hz; words: 1.1-4.5 Hz; syllables: 1.7-26.1 Hz), see Figure A (Supplemental Materials) for a visualization of results.

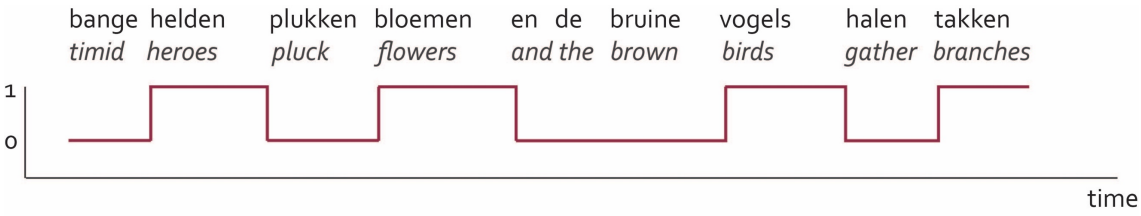

Figure 3. Visualization of the phrase-level annotations (inspired by Fig.2 in Brodbeck et al., 2018). Across time, the response array takes value 0 for words that cannot (yet) be integrated into phrases, and value 1 for words that can, resulting in a "pulse train" array.

Mutual Information Analysis

We used Mutual Information (MI) in order to quantify the statistical dependency between the phase of speech envelopes and the EEG recordings according to the procedure described in Keitel et al. (2018; see also Gross et al., 2013; Kayser et al., 2015; Keitel et al., 2017). Based on the previously identified frequency bands of interest (see section "Speech preprocessing" above), we filtered both speech envelopes and EEG signals in each band (third-order Butterworth filter, forward and reverse). We then computed the Hilbert transform in each band and used the part of the Hilbert transform corresponding to the phase information (see Ince et al., 2017, for details) for further analysis. This resulted in two sets of two-dimensional variables (one for speech signals and one for EEG responses) in each condition (forward and backward; again, see Ince et al., 2017, for a more in-depth description). To take brain-stimulus lag into account, we computed MI at 5 different lags, ranging from 60 to 140 ms in steps of 20 ms, and to exclude auditory evoked responses we excluded the first 200 ms of each stimulus-signal pair. MI values from all five lags were averaged for subsequent statistical evaluation. We further concatenated all trials from speech and brain signals in order to increase the robustness of MI computation (Keitel et al., 2018).

In order to test whether the statistical dependency between the speech envelope and the EEG data as captured by MI was modulated by the linguistic structure and

content of the stimulus, we compared phase MI values in all three frequency bands separately. Linear mixed models were fitted to the log-transformed, trimmed (5% on each end of the distribution) MI values in each frequency band using lme4 (Bates et al., 2015) in R (R Core Team, 2018). Models included main effects of Condition (three levels: Sentence, Wordlist, Jabberwocky) and Direction (two levels: Forward, Backward), as well as their interaction. All models included by-participant random intercepts and random slopes for the Condition * Direction interaction. For model coefficients, degrees of freedom were approximated using Satterthwaite's method as implemented in the package lmerTest (Kuznetsova, Brockhoff & Christensen, 2017). We used treatment coding in all models, with Sentence being the reference level for Condition, and Forward the reference level for Direction. We then computed all pairwise comparisons within each direction using estimated marginal means (Tukey correction for multiple comparisons) with emmeans (Length, 2018) in R (i.e., comparing Sentence Forward to Jabberwocky Forward and Wordlist Forward, but never Sentence Forward to Jabberwocky Backward, because we had no hypotheses about these comparisons). See Supplemental Materials for complete model outputs.

For the exploratory dimensionality-reduced MI analysis, we performed the same set of statistical analyses (but only in one single frequency band). Specifically, we fitted a linear mixed model including main effects of Condition (three levels: Sentence, Wordlist, Jabberwocky) and Direction (two levels: Forward, Backward), as well as their interaction and by-participant random intercepts and random slopes for the Condition * Direction interaction to the log-transformed, trimmed phase MI values. We then computed estimated marginal means precisely as described in the previous section.

Finally, in order to analyze whether phase MI was statistically higher at lower frequency bands, corresponding to more structured linguistic representations, we

repeated the statistical analysis described above, but this time submitting the phase MI values from all three frequencies to a single mixed model that included fixed effects of Direction and Frequency, as well as their interaction and random by-participant intercepts. Again, degrees of freedom were approximated using Satterthwaite's method as implemented in the package lmerTest (Kuznetsova, Brockhoff & Christensen, 2017). We used treatment coding in the model, with the syllable level being the reference level for Frequency, and Forward the reference level for Direction. We then computed all pairwise comparisons within each direction using estimated marginal means (Tukey correction for multiple comparisons) with emmeans in R as previously (Length, 2018).

Results

Speech tracking. We computed Mutual Information (MI) between the phase of the Hilbert-transformed EEG time series and the phase of the Hilbert-transformed speech envelope within three frequency bands of interest that corresponded to the occurrence rates of phrases (0.8-1.1 Hz), words (1.9-2.8 Hz), and syllables (3.5-5.0 Hz). These frequency bands were identified based on annotations of the stimuli (see Figure 1, Table 1, and section "Materials and methods" for further details and example stimuli) in a cluster of central electrodes.

Specifically, we designed our experiment to assess whether the brain response is driven by the (quasi-)periodic temporal occurrence of linguistic structures, or whether it is modulated as a function of the *content* of those structures. Using MI allowed us to quantify and compare the degree of speech tracking across sentences, word lists, and jabberwocky items.

We found condition-dependent enhanced phase MI at distinct timescales (see Figure 2). In the phrase frequency band (0.8-1.1 Hz), phase MI was significantly higher for sentences compared to jabberwocky items and word list (Sentence – Jabberwocky: Δ

= 0.50, SE = 0.10, $p < 0.01$; Sentence – Wordlist: $\Delta = 0.40$, SE = 0.12, $p < 0.01$; all results Tukey corrected for multiple comparisons); in the word frequency band (1.9-2.8 Hz), MI was significantly higher for sentences compared to jabberwocky items (Sentence – Jabberwocky: $\Delta = 0.38$, SE = 0.12, $p = 0.01$). None of these effects were present in the backward speech, demonstrating that they are not driven by the acoustic properties of the stimuli (see section Materials and Methods for details about our mixed effects models structures; see Supplemental Materials – Tables 1a, 1b, 2a and 2b – for complete model outputs). Note also that the likelihood ratio tests (comparable to the interaction term in classical repeated-measures Anova) revealed a significant interaction between Condition and Direction in the phrase frequency band ($\chi^2(2) = 6.25$, $p = 0.04$); on the word timescale, the pair-wise differences between the forward conditions were simple effects (word level: $\chi^2(2) = 0.98$, $p = 0.61$). An almost identical pattern of results also emerged when computing MI over all electrodes (rather than a cluster of central ones), with sentences showing higher MI than jabberwocky items and word lists both in the phrase band (Sentence – Jabberwocky: $\Delta = 0.36$, SE = 0.08, $p < 0.01$; Sentence – Wordlist: $\Delta = 0.31$, SE = 0.09, $p < 0.01$) and in the word frequency band (Sentence – Jabberwocky: $\Delta = 0.33$, SE = 0.09, $p < 0.01$; Sentence – Wordlist: $\Delta = 0.14$, SE = 0.05, $p = 0.01$). Again, we found no significant differences between the backward controls when computing MI over the entire head. These findings indicate that neural tracking is enhanced for linguistic structures at timescales specific to that structure's role in the unfolding meaning of the sentence, consistent with neurophysiologically inspired models of language comprehension (Martin, 2016; Martin & Doumas, 2017).

Like previous studies (e.g., Gross et al. 2013; Kayser et al., 2015; Keitel et al., 2018), we also found significantly higher phase MI in lower frequency bands, corresponding to higher-level linguistic units such as phrases, compared to the word and

syllable frequency bands (see Figure 2; phrase – word: $\Delta = 0.76$, SE = 0.08, $p < 0.01$; phrase – syllable: $\Delta = 1.66$, SE = 0.08, $p < 0.01$ word – syllable: $\Delta = 0.91$, SE = 0.08, $p < 0.01$). These results might suggest that the brain response is largely driven by information present at lower frequency bands, rather than tracking of the syllable envelope. Note, however, that we found the same significant effects for comparisons between the backward conditions (phrase – word: $\Delta = 0.60$, SE = 0.08, $p < 0.01$; phrase – syllable: $\Delta = 1.08$, SE = 0.08, $p < 0.01$; word – syllable: $\Delta = 0.47$, SE = 0.08, $p < 0.01$). Although the effects appear to be more pronounced for forward than for backward conditions, as evidenced by a significant positive Frequency * Direction interaction in the base model ($\chi^2(2) = 26.29$, $p < 0.01$; based on likelihood ratios), it is unclear whether increased MI at lower frequencies reflects increased sensitivity of the brain to information occurring at those frequencies, or whether these effects are due to properties of the acoustic signal and/or related to the 1/f frequency component (see Ouyang et al., 2019, for a more detailed discussion of the potential confounds of 1/f brain activity).

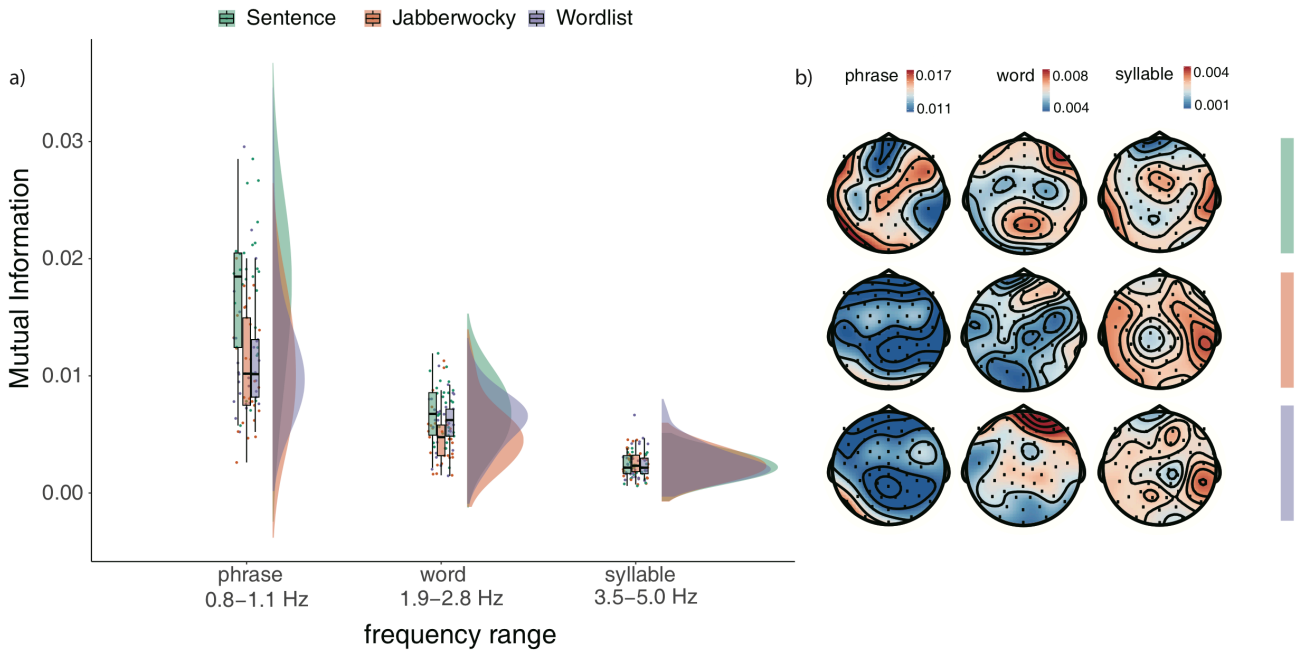

Figure 3. Phase MI between speech signal and brain response. Panel a) shows MI for Sentences (green), Jabberwocky items (orange), and Word lists (purple) for phrase, word and syllable timescales across central

electrodes (each dot represents one participant's mean MI response averaged across electrodes). Panel b) shows the average scalp distribution of MI per condition and band, averaged across participants. Raincloud plots were made using the Raincloud package in R (Allen et al., 2019).

Tracking of abstract linguistic units. Inspecting the modulation spectra of our stimuli (Figure 2), it is apparent that – although carefully designed – the acoustic signals are not entirely indistinguishable between conditions based on their spectral properties. Most notably, Sentence stimuli appear to exhibit a small peak at around 0.5 Hz (roughly corresponding to the phrase timescale in our stimuli) compared to the other two conditions. It is important to note that (1) differences between conditions are not surprising, given that our stimuli were naturally spoken, and (2) we specifically designed our experiment to include backward versions of all conditions to control for slight differences between the acoustic envelopes of the forward stimuli. That being said, we conducted an additional, exploratory analysis of the phrase frequency band in order to further reduce the potential confound of differences between the acoustic modulation spectra, and to disentangle the distribution of linguistic phrase representations and the acoustic stimulus even further.[3] Specifically, we computed phase MI in the delta-theta range (0.8-5 Hz) between the brain response and abstracted, dimensionality-reduced annotations of all stimuli, containing only information about when words could be integrated into phrases (cf. Brodbeck, Presacco & Simon, 2018; see section Materials and Methods for detailed descriptions of how these annotations were created). These annotation-based analyses revealed increased phase MI for sentences compared to jabberwocky items and word lists (Sentence – Jabberwocky: $\Delta = 0.33$, SE = 0.10, $p < 0.01$; Sentence – Word list: $\Delta = 0.52$, SE = 0.11, $p < 0.01$; all results Tukey corrected for multiple comparisons) and no significant difference among the backward controls (see Supplemental Materials for complete model outputs). Again,

[3] We thank an anonymous reviewer for inspiring this exploratory analysis.

the same pattern of results also emerged when computing MI over all electrodes (Sentence – Jabberwocky: $\Delta = 0.35$, SE = 0.08, $p < 0.01$; Sentence – Word list: $\Delta = 0.62$, SE = 0.11, $p < 0.01$). These results support our previously reported findings, showing that phase alignment is influenced by the presence of abstract linguistic information. In other words, this exploratory analysis supports our earlier finding that the brain's "sensitivity" to linguistic structure and meaning goes above and beyond the acoustic signal.

Discussion

The current experiment tested how the brain attunes to inferred linguistic information that is not physically encoded in the acoustic properties of the stimulus in a straight-forward manner. Contrasting sentences, word lists and jabberwocky items, we analyzed, by proxy, how the brain response is modulated by sentence-level prosody, lexical semantics, and compositional structure and meaning. Our findings show that 1) the neuronal response is driven by compositional structure and meaning, beyond both acoustic-prosodic and lexical information; and 2) the brain most closely tracks the most structured representations on each of the distinct timescales we analyzed. We discuss these findings in more detail below.

Using Mutual Information analysis, we quantified the degree of speech tracking in frequency bands corresponding to the timescales at which linguistic structures (phrases, words, and syllables) occurred in our stimuli. Specifically, we compared neuronal tracking of phrases, words and syllables (as evidenced by MI) between sentences, jabberwocky items, and word lists.

On the phrase timescale, we found that sentences had the most shared information between stimulus and response, which could reflect the importance of both prosodic and compositional semantic structure during sentence comprehension. Crucially, this is not

merely about chunking – participants could have “chunked” the word lists (which have their own naturally produced non-sentential prosody) into units of adjacent words, and the jabberwocky items into prosodic units. Instead, we argue that, on the timescale of phrases, the dominating process appears to be processing of compositional semantic structure, above and beyond prosodic chunking and word-level meaning.

To reiterate, we do not take the observed increase in MI for sentences compared to jabberwocky items and word lists as evidence for an intrinsic “phrase- “, or “sentence-level oscillator”. Rather, we interpret the graded differences in MI at this timescale as a manifestation of the cortical computations that may occur during language comprehension – here, we observe them in the delta frequency range because that is the timescale on which higher-level linguistic units occur in our stimuli. Meaning and structure do not exhibit straight-forward diagnostic physical manifestations in the acoustic signal, so if one commits to a strictly physiological view where “tracking” is, by definition, a response to rhythmic regularities of an extrinsic stimulus (e.g., Schroeder & Lakatos, 2009), it is unclear what the brain really “tracks” when it comes to higher-level linguistic units. In line with linguistic models of cue integration (Martin, 2016; Martin & Doumas, 2017), we argue that neuronal tracking can indicate the alignment of oscillatory brain responses to both external, stimulus-driven information (e.g., the amplitude envelope of the speech signal) *and* internal, inferred information (e.g., linguistic units such as words, phrases and sentences). Crucially, our experiment shows that the observed phase alignment of neural responses to inferred linguistic structures is not simply driven by the (quasi-)periodic occurrence of these structures at a given frequency: Both sentences and jabberwocky stimuli contained periodically occurring “phrases”, but our results show that the brain aligns more to those periodically occurring units when they contain meaningful information and are thus

relevant for linguistic processing. These phase MI results are further corroborated by an additional, exploratory analyses using abstracted linguistic annotations of the stimuli (cf. Brodbeck et al., 2018). Phase alignment in the frequency range of phrases thus appears to reflect more than a mere chunking of the signal into units (e.g., Bonhage et al., 2017; Ghitza, 2017).

On the word timescale, we found significantly higher MI between stimulus and brain response for sentences compared to jabberwocky items. We tentatively take this finding to indicate that, at the word timescale, the dominant process appears to be context-dependent word recognition – perhaps based in perceptual inference. Interestingly, we also found enhanced MI on the word timescale between stimuli and brain response for word lists compared to jabberwocky items when computing MI over all electrodes. Here, listeners would not have been able to integrate words into phrases or sentences, which makes it somewhat difficult to integrate these results.

For the syllable-level timescale, we found no phase MI effects between the three forward conditions. We did find enhanced MI for forward compared to backward conditions, which is in line with previous findings, showing that tracking of the syllable envelope is enhanced for intelligible and attended speech (e.g., Peelle & Davis, 2012; Teng, Tian, Doelling, & Poeppel, 2018; Zoefel, ten Oever, & Sack, 2018). This could be due to envelope-tracking in the delta-theta band being facilitated by sharp edges in the acoustic signal, or "acoustic landmarks" (Doelling et al., 2014).

One important point to note is that not all the studies investigating "phase alignment" (for lack of a better word) used the same measures. Here, we report results from MI analysis. Other approaches measure the coherence between phase angles across trials to quantify coherence *within* one signal. In contrast to this, MI and other methods, such as Cerebro-Acoustic Coherence (e.g., Doelling et al., 2014; Peelle et al.,

2012), capture the similarity *between* two signals. It is important to distinguish between these different measures of "phase alignment", as they might yield slightly different results – populations of neurons firing "in phase" with each other does not necessarily imply being "in phase" with an external stimulus. We hope that future work will investigate in detail how phase similarity patterns *within the brain* relate to phase similarity patterns *between brain and stimulus* (as captured by measures such as MI and Cerebro-Acoustic Coherence), and which of these techniques can provide an adequate measure of neural tracking or "entrainment" to language. Even more generally, we would be very interested to investigate in more detail how to bridge the perceived conceptual "gap" between experiments observing increased brain-stimulus phase similarity on the one hand (e.g., the current experiment; Keitel et al., 2018; Gross et al., 2013) and experiments observing increased spectral power in the M/EEG signal that goes *beyond* the acoustic signal, possibly related to "structure-building" (e.g., Ding et al., 2016, 2017). In the current experiment, we believe that MI provides a straight-forward measure of linguistic inference; the listener can only be able to attune to the acoustic signal more closely at timescales that are relevant for comprehension *based on* inferred linguistic information, which is not apparent to the listener based solely on the acoustic signal.

Many previous studies have shown that attention can modulate neural entrainment (e.g., Calderone et al., 2014; Lakatos et al., 2013; Golumbic et al., 2013; Ding & Simon, 2012). Importantly, Ding et al. (2018) found that attention to a speech stimulus is required in order for neural tracking beyond the syllable envelope to be observed, suggesting that combining syllables into words and phrases requires attention. In our current experiment, participants were instructed to attentively listen to the audio recordings in all conditions, but it is, in principle, possible that "attending to sentences"

might be easier than “attending to jabberwocky items”, and that listeners are generally more likely to pay attention to higher-level structures in intelligible and meaningful speech. As such, we cannot rule out the possibility that our effects might be influenced to some extent by a mechanism that is based on attentional control. Note, however, that it is very difficult to disentangle “attention” from “comprehension” in this kind of argument – we would argue that meaningful information within a stimulus can only lead to increased attention if it is comprehensible. In a similar vein, one could argue that the observed increases in MI at distinct timescales for different conditions might be readily explained by changes in working memory load. Just as for attention-driven mechanisms, we acknowledge that a mechanism based on working memory cannot entirely be ruled out given our current results, but again, we would argue that it is very difficult to isolate “comprehension” from “working memory load”, as working memory effects can only arise as a result of comprehension. We plan to investigate these interesting questions in more detail in future experiments.

Overall, the pattern of results is consistent with cue-integration-based models of language processing (Martin, 2016), where the activation profile of different populations of neurons over time is what encodes the linguistic structure as it is inferred from sensory correlates in real-time (Martin & Doumas, 2017). Martin’s (2016) model of language processing is based on neurophysiological models of cue integration, which have been investigated in depth in the fields of visual and multisensory perception (e.g., Ernst & Bülthoff, 2004; Fetsch, DeAngelis, & Angelaki, 2013; Landy, Banks, & Knill, 2011; see Toscano & McMurray, 2015; and Norris & McQueen, 2008, for cue-integration-based models of speech and word recognition). The underlying mechanism of cue integration relies on only two core computations: summation and normalization, both of which have been proposed as canonical neural computations (e.g., Carandini &

Heeger, 1994, 2012). Multiple cues (which can, in principle, be any piece of sensory information that is available in a given situation) are combined via summation and integrated via normalization in order to arrive at a robust percept (e.g., Ernst & Bülthoff, 2004). Cues are associated with corresponding weights, which can be dynamically updated in order to account for the fact that not all cues are equally reliable (or even available) in any given situation (see also Bates & MacWhinney, 1989, and Bornkessel & Bornkessel-Schlesewsky, 2006, for models of sentence processing that posit competition between different linguistic percepts as a result of cue validity and ranking). As such, the process of integrating multiple cues into a percept can be thought of as an inference problem (e.g., Landy et al., 2011). Martin (2016) proposed that, during all stages of language processing, the brain might draw on these same neurophysiological computations. Crucially, inferring linguistic representations from speech sounds requires not only bottom-up, sensory information, but also top-down, memory-based cues (e.g., Marslen-Wilson, 1987; Martin, 2016; Kaufeld et al., 2019). Martin (2016) therefore suggested that cue integration during language comprehension is an iterative process, where cues that have been inferred from the acoustic signal can, in turn, become cues for higher levels of processing. For example, phonemes that have been inferred from acoustic cues in the speech signal can act as cues for inferring syllables, which can, in turn, act as cues for words, phrases, and so on. As such, the pattern of findings in our current experiment strongly speaks to cue-integration-based models of language comprehension: We observe that neuronal tracking of the speech signal is enhanced for timescales on which meaningful linguistic units can be inferred, suggesting that phase alignment of populations of neurons might, indeed, encode the generation of inference-based linguistic representations (Martin & Doumas, 2017).

Our results also speak to analysis-by-synthesis-based accounts of speech processing more generally (e.g., Bever & Poeppel, 2010; Halle & Stevens, 1962; Poeppel & Monahan, 2011). In an analysis-by-synthesis model of speech perception, speech recognition is achieved by internally generating (*synthesizing*) patterns according to internal rules and matching (*analyzing*) them against the acoustic input signal. This bears striking similarities to cue integration, although one might argue that the underlying computations and the neural implementation of analysis-by-synthesis are not sufficiently specified. In our view, cue-integration-based models of language processing such as the one suggested by Martin (2016) offer the most promising framework for our findings because they make explicit predictions about both the oscillatory patterns of populations of neurons during the inference process, and about the neurophysiological computations potentially underlying these patterns.

We found that phase alignment was significantly enhanced for higher-level linguistic structures, such as phrases, as opposed to syllables. These results are in line with previous findings from Keitel et al. (2018; see also Gross et al., 2013), who reported higher degrees of MI in the delta compared to the theta frequency band, corresponding to the frequency in which the most structured representations occurred in their stimuli. However, because we observed the same pattern of effects for forward *and* backward conditions, our data cannot speak to *why* tracking is enhanced at lower frequencies, and whether this is mainly due to confounds with 1/f brain activity (cf. Ouyang et al., 2019). Still, we find these results striking, especially considering the accumulating evidence that the most *acoustically* prominent information appears to occur at the frequency of the syllable. Ding et al. (2017b), for example, have shown that modulation spectra across languages consistently show a prominent peak at around 4 Hz. Why is it, then, that the brain response does not align most closely to the parts of

the acoustic signal that are most prominent? Exploring in more detail why MI between brain and acoustic signal appears to be consistently highest at lower frequencies will be an interesting avenue for future research. To that end, we believe that studying naturalistic stimuli will further enhance our understanding of spoken language comprehension (Alday, 2019; see also Alexandrou et al., 2018).

There are, of course, many other open questions that arise from our results. Perhaps most obviously (although presumably limited by the resolution of time-frequency analysis), it would be interesting to investigate how "far" cue integration can be traced during more natural language comprehension situations (cf. Alday, 2019, Alexandrou et al., 2018). To what degree are higher-level linguistic cues, such as sentential, referential, contextual, or pragmatic information, encoded in the neural response? Another interesting avenue for future research would be to investigate whether similar patterns can be observed during language production. Martin (2016) suggested that not only language comprehension, but also language production draws on principles of cue integration. Similarly, analysis-by-synthesis-based accounts suggest that the "generation rules" used to synthesize candidate representations that the sensory signal can be matched against are, in essence, identical to the rules used for language production. Observing similar oscillatory patterns during language production experiments (cf. Watanabe et al. 2019), where speakers are actively generating linguistic units, would yield strong supporting evidence for analysis-by-synthesis- and cue-integration-based accounts of language processing. Finally – and consequentially, if cue integration underlies both comprehension and production processes –, we would be curious to learn more about cue integration "in action", specifically during dialogue settings, where interlocutors comprehend and plan utterances nearly simultaneously.

In summary, this study showed that speech tracking is sensitive to both linguistic structure and meaning, above and beyond the frequency at which they occur in the stimulus. In other words: Content determines tracking, not just timescale. This extends previous findings and advances our understanding of spoken language comprehension in general, because our experimental manipulation allows us, for the first time, to disentangle the influence of linguistic structure and meaning on the neural response from the timescales at which that linguistic information occurs in the input. Cue-integration-based models of language processing (Martin, 2016; Martin & Doumas, 2017) offer a neurophysiologically plausible, mechanistic explanation for our results.

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Supplemental Material

Stimuli

1. *Sentence*: Vlotte meesters schenken wijsheid en een aardig kindje schildert sterren.
   (Chatty teachers offer wisdom and a nice child paints stars.)
   Jabberwocky: Snatte waasters scharken wielheid en een aallig wundje schurdert sperben.
   Word list: schildert schenken vlotte aardig wijsheid kindje meesters sterren en een

2. Gekke meisjes snijden uien en de scherpe messen maken wondjes.
   (Crazy girls cut onions and the sharp knives cause wounds.)
   Gelpe muikjes floeden euer en de strerbe letsen lapen wouwses.
   uien wondjes meisjes messen de en snijden maken gekke scherpe

3. Kleine obers tapten biertjes en de domme gasten breken borden.
   (Little waiter tapped beers and the stupid guests break plates.)
   Spiene abels pipten beeltjes en de lolme gonten flepen varden.
   tapten breken kleine domme de en borden obers biertjes gasten

4. Lange mannen bouwen huisjes en de lieve honden brengen planken.
   (Tall men build houses and the sweet dogs bring boards.)
   Lalve wanzen botren raasjes en de reeve rorden brargen sponken.
   planken mannen huisjes honden de en bouwen brengen lange lieve

5. Trotse moeders hebben baby's en de lieve oma's geven snoepjes.
   (Proud mothers have babies and the sweet grandmas give sweets.)
   Pletse hijders rabben obis en de rieze bawun beben vliepjes.
   hebben geven trotse lieve de en snoepjes moeders baby's oma's

6. Goede sporters renden rondjes en de grote wolken bieden schaduw.
   (Good athletes ran laps and the big clouds provide shadow.)
   Vijde spenters rarden rouwses en de spode delken vuiden scharub.
   schaduw sporters rondjes wolken de en renden bieden goede grote

7. Stoute muizen knagen gaten en de boze huurders haten dieren.
   (Naughty mice gnaw holes and the angry tenants hate animals.)
   Stemte mieven snamen vaden en de vone hinkders doten weiren.
   knagen haten stoute boze de en gaten muizen huurders dieren

8. Slimme eekhoorns vinden nootjes en de groene kikkers vangen vliegjes.
   (Smart squirrels find nuts and the green frogs catch flies.)
   Plemme oekboorns ganden zietjes en de broeze wokkers gongen snoegjes.
   eekhoorns nootjes kikkers vliegjes de en vinden vangen slimme groene

9. Bange ridders zoeken toevlucht en de gouden sleutel opent deuren.
   Frightened knights seek refuge and the golden key opens doors.)
   Garge ludders nijken toepricht en de gatden speetel ogens weiren.
   zoeken opent bange gouden de en sleutel ridders toevlucht deuren

10. Blauwe visjes zwemmen baantjes en de grijze kippen horen piepjes.
    (Blue fish swim laps and the grey chickens hear beeps.)
    Braube bispes knimmen gaantres en de brijne dappen lolen peugjes.
    kippen visjes baantjes piepjes de en zwemmen horen blauwe grijze

11. Grote leeuwen vinden voedsel en de jonge schapen blijken geitjes.
    (Big lions find food and the young sheep turn out to be goats.)
    Spode loorden ginten baadsel en de jarge straben ploeken gaukjes.
    vinden lijken grote jonge de en voedsel leeuwen schapen geitjes

12. Kwade jongens breken glazen en de strenge juffen schrijven regels.
    (Evil boys break glasses and the strict teachers write rules.)
    Smate jargens drepen flaven en de strelle ceffen schroezen lemels.
    jongens juffen glazen regels de en breken schrijven kwade strenge

13. Zieke kindjes krijgen appels en de kalme zusters breien sokken.
    (Sick children get apples and the calm sisters knit socks.)
    Neike wundjes spijmen atsels en de malge nutters pleuen senken.
    krijgen breien zieke kalme de en kindjes appels zusters sokken

14. Warme landjes hebben strandjes en de korte dagen brengen vreugde.
    (Warm lands have beaches and the short days bring joy.)
    landjes strandjes dagen vreugde de en hebben brengen warme korte
    Marle lerkjes mobben strastpes en de warte lapen spelgen fleufde.

15. Zwarte geiten proefden suiker en de rotte tanden hebben gaten.

(Black goats taste sugar and the rotten teeth have holes.)
Flakte beuten praasden feeker en de hatte palden mabben voten.
proefden hebben zwarte rotte de en gaten geiten suiker tanden

16. Rode mieren dragen takken en de wilde katten vangen vogels.
(Red ants carry branches and the wild cats catch birds.)
Lote keeren tramen tenken en de kelde lutten gargen valmen.
takken mieren katten vogels de en dragen vangen rode wilde

17. Grauwe wolken brengen regen en de zware buien breken takken.
(Grey clouds bring rain and the heavy showers break branches.)
Kraube louken pletgen lepen en de plave gijen smesen tonken.
brengen breken grauwe zware de en buien wolken regen takken

18. Blije artsen helpen mensen en de oude tantes hebben nichtjes.
(Happy doctors help people and the old aunts have nieces.)
Ploeie alfjen hospen miksen en de aide paltes labben zechtjes.
artsen mensen tantes nichtjes de en helpen hebben oude blije

19. Houten tafels hebben laatjes en de ronde knikkers lijken druiven.
(Wooden tables have drawers and the round marbles look like grapes.)
Hemten pacels libben raakjes en de dande vlokkers woeken driezen.
lijken houten hebben ronde de en tafels laatjes knikkers druiven

20. Zwarte laarzen trekken aandacht en de vreemde mannen schrobben vloeren.
Black boots attract attention and the strange men are scrubbing floors.)
Knorte raarnen grikken aangucht en de smijmde lonnen schrimben knijren.
vloeren laarzen aandacht mannen de en trekken schrobben zwarte vreemde

21. Snelle jagers volgen spoortjes en de tamme hazen leggen keutels.
(Fast hunters follow tracks and the tame hares lay turds.)
Flolle cavers valmen vleertjes en de torme lamen lelmen weitels.
volgen leggen snelle tamme de en jagers spoortjes keutels hazen

22. Leuke otters zoeken visjes en de grote leeuwen bijten mensen.
(Nice otters look for fish and the big lions bite people.)
Rauke akters nijken vaspes en de plode loorten gijden molsen

leeuwen otters visjes mensen de en zoeken bijten leuke grote

23. Stille meisjes mengen sapjes en de rijke zeilers slurpen koffie.
(Silent girls mix juices and the rich sailors sip coffee.)
Stimpe muikjes lelgen sekjes en de lijse neulers plunpen wiffie.
mengen slurpen stille rijke de en zeilers meisjes sapjes koffie

24. Trotse slagers snijden biefstuk en de blije klanten kopen worstjes.
(Proud butchers cut beef and the happy customers buy sausages.)
Bletse tramers proeden vaafstuk en de knoeie sponten women wuchtjes.
biefstuk worstjes klanten slagers de en snijden kopen trotse blije

25. Knappe schilders winnen prijsjes en de wilde paarden aten peren.
(Handsome painters win prizes and the wild horses eat pears.)
Flippe scharders dinzen proekjes en de kelde deurden usen remen.
winnen aten knappe wilde de en schilders prijsjes paarden peren

26. Stompe messen snijden broodjes en de paarse pennen schrijven woorden.
(Blunt knives cut sandwiches and the purple pens write words.)
Starpe retsen knoeden braaljes en de waadse parnen schroezen moorten.
messen broodjes pennen woorden de en snijden schrijven stompe paarse

27. Bruine apen zoeken vruchten en de witte schapen aten blaadjes.
(Brown monkeys seek fruit and the white sheep eat leaves.)
Driene onen nijken smechten en de kette straven oken bleegjes.
zoeken aten bruine witte de en apen schapen blaadjes vruchten

28. Oude opa's snoeien heggen en de lieve oma's bakten koekjes.
(Old grandpas prune hedges and the sweet grandmas baked cookies.)
Adde obos knooien relgen en de ruive onis borten moefjes.
koekjes opa's heggen oma's de en snoeien bakten oude lieve

29. Trieste zwemmers schrijven brieven en de lompe zangers zingen liedjes.
(Sad swimmers write letters and the rude singers sing songs.)
Breeste knimmers schroezen pleiven en de laspe zallers zannen riefjes.
schrijven zingen trieste lompe de en brieven liedjes zangers zwemmers

30. Stoere vaders prikken gaten en de vlotte moeders koken uien.
    (Tough fathers poke holes and the chatty mothers cook onions.)
    Stijne gaters drekken vaden en de knette hijders mosen auer.
    moeders vaders gaten uien de en prikken koken stoere vlotte

31. Mooie vogels zingen wijsjes en de gekke meiden wassen kleren.
    (Beautiful birds sing tunes and the crazy girls wash clothes.)
    Woeie govels zanpen waadjes en de gesse kieden pansen pleven.
    zingen wassen mooie gekke de en vogels wijsjes kleren meiden

32. Knappe zangers geven feestjes en de stoere werklui kopen biertjes.
    (Handsome singers give parties and the tough workers buy beers.)
    Smippe zalpers beben feursjes en de steepe werfmui rogen booltjes.
    zangers werklui biertjes feestjes de en geven kopen knappe stoere

33. Vieze kwallen prikken duikers en de dunne vissers huurden bootjes.
    (Dirty jellyfish sting divers and the thin fishermen rented boats.)
    Beeze flollen kwokken keekers en de murne bitsers lutsden boepjes.
    prikken huurden vieze dunne de en duikers vissers bootjes kwallen

34. Sterke vaders dragen dochters en de mooie meisjes zoenden jongens.
    (Strong fathers carry daughters and the beautiful girls kissed boys.)
    Sperre goders tramen wichters en de moene miekjes nienden jorlens.
    dochters meisjes vaders jongens de en dragen zoenden sterke mooie

35. Lompe kappers knippen haren en de vlugge klussers bouwen muren.
    (Rude hairdressers cut hair and the quick handymen built walls.)
    Lolle mippers vrappen lalen en de snigge spessers botren luven.
    knippen bouwen lompe vlugge de en muren kappers klussers haren

36. Leuke vrouwen spelen cello en de dikke drummers poetsten trommels.
    (Nice women play cello and the fat drummers cleaned drums.)
    Mauke smouven pleren jeldo en de wokke plurmers peursten spolmels.
    vrouwen drummers cello trommels de en spelen poetsten leuke dikke

37. Arme vrouwen poetsten schoenen en de trage laptops brengen spanning.
    (Poor women polished shoes and the slow laptops cause tension.)

Orle vrulwen poonsten scheemen en de drame lanteps spelgen klanzing.
poetsten brengen arme trage de en vrouwen spanning schoenen laptops

38. Lieve meisjes plukten appels en de schuwe jongens vrezen hoogtes.
(Sweet girls picked apples and the shy boys are afraid of heights.)
Reeve muipjes slunten atjels en de schine jargens flenen haaites.
meisjes hoogtes appels jongens de en plukten vrezen lieve schuwe

39. Drukke winkels lokten klanten en de lange mannen kopen schoenen.
(Busy stores attracted customers and the tall men buy shoes.)
Spunke linsels lurten spalten en de lalve wanzen loben scheegen.
lokten kopen drukke lange de en winkels klanten schoenen mannen

40. Gekke jongens pesten eenden en de zieke meiden poetsten tanden.
(Crazy boys harrass ducks and the sick girls brushed their teeth.)
Gelse jormens tetten oelden en de neike kieden peugsten palden.
tanden jongens meiden eenden de en pesten poetsten gekke zieke

41. Vreemde vrouwen hebben heimwee en de trouwe buren zenden brieven.
(Strange women are homesick and the loyal neighbors send letters.)
Smuimde flouven rabben heipwij en de blouve guven zarden pleiven.
hebben zenden vreemde trouwe de en heimwee vrouwen brieven buren

42. Kleine baby's horen liedjes en de wijze kerels lezen kranten.
(Small babies hear songs and the wise guys read newspapers.)
Speune bawus ronen riefjes en de moeze lenels remen sponten.
baby's kerels liedjes kranten de en horen lezen kleine wijze

43. Saaie buren kopen borden en de jonge kindjes pakten snoepjes.
(Boring neighbors buy plates and the young children grabbed sweets.)
Siere gulen loben girden en de jelge wirtjes penten vloesjes.
pakten saaie kopen jonge de en buren borden kindjes snoepjes

44. Snelle schaatsers vinden gaatjes en de kleine jongens spelen voetbal.
(Fast skaters find holes and the little boys play soccer.)
Flolle schijnsers ginten geekjes en de speene jargens sleren boenbel.
schaatsers voetbal gaatjes jongens de en vinden spelen snelle kleine

45. Witte paarden trekken koetsen en de saaie vorsten wenkten burgers.
    (White horses pull carriages and the boring monarchs greet civilians.)
    Kette peenden drakken dietsen en de soene viksten lankten vurmers.
    trekken wenkten witte saaie de en paarden vorsten burgers koetsen

46. Stille schilders belden vrienden en de roze scooter levert pizza.
    (Quiet painters called friends and the pink scooter delivers pizza.)
    Stimpe schadders benten fleunden en de lone sjaater rezert pixta.
    schilders scooter vrienden pizza de en roze stille levert belden

47. Oude mensen rijden bussen en de toffe oma's maken grapjes.
    (Old people ride busses and the cool grandmas make jokes.)
    Amde molsen mieden gossen en de puffe onos lapen spipjes.
    rijden maken oude toffe de en bussen grapjes oma's mensen

48. Brede tantes zoenden wangen en de malle neven roken jointjes.
    (Sturdy aunts kissed cheeks and the silly nephews smoked joints.)
    Krete pastes noonden largen en de kolle zeben kosen jarstjes.
    wangen neven jointjes tantes de en zoenden roken brede malle

49. Jonge bakkers maken broden en de nette klanten ruiken taartjes.
    (Young bakers make bread and the neat customers smell cake.)
    Jorle bassers hapen smoten en de zutte spalten hieken toordjes.
    maken ruiken jonge nette de en broden taartjes klanten bakkers

50. Klamme handen voelen muren en de knusse kachels drogen kleren.
    (Damp hands feel walls and the cozy ovens dry clothes.)
    Klorme londen vijren luven en de vresse maspels blomen spemen.
    handen muren kachels kleren de en voelen drogen klamme knusse

51. Snelle zwemmers slurpen ijsthee en de vieze kwallen zoeken water.
    (Fast swimmers slurp iced tea and the dirty jellyfish look for water.)
    Knille knummers plunpen ijfkwee en de bieve smollen nijken lates.
    slurpen zoeken vieze snelle de en zwemmers ijsthee kwallen water

52. Bange helden plukken bloemen en de bruine vogels halen takken.
(Frightened heroes pick flowers and the brown birds fetch branches.)
Garge ralden spunken drijmen en de druize gomels paven mukken.
helden bloemen vogels takken de en plukken halen bange bruine

53. Vlotte otters bouwen dammen en de snelle hazen doden kevers.
(Smooth otters build dams and the fast hares kill beetles.)
Zwitte olders botren lemmen en de vralle lamen zoten mezers.
bouwen doden vlotte snelle de en otters dammen hazen kevers

54. Saaie meesters geven lessen en de vele brieven worden stapels.
(Boring teachers give lessons and the many letters become piles.)
Soene waasters beben hussen en de bene pleeven rarden stagelt.
meesters lessen stapels brieven de en geven worden saaie vele

55. Luikse wafels stillen honger en de rotte appels krijgen schimmel.
(Liège waffles satisfy hunger and the rotten apples are getting moldy.)
Ruipre lafelt stimpen morger en de hatte ampelt spijmen schurmel.
krijgen stillen luikse rotte de en wafels honger appels schimmel

56. Enge slangen eten muizen en de grote kippen leggen eitjes.
(Scary snakes eat mice and the big chickens lay eggs.)
Elme spalgen eber mienen en de vlode dappen relgen eutres.
slangen muizen kippen eitjes de en eten leggen enge grote

57. Scherpe scharen knippen blaadjes en de snelle auto's rijden rondjes.
(Sharp scissors cut leaves and the fast cars drive laps.)
Strerbe stranen smeppen bleegjes en de flalle euvos loeden lortjes.
knippen rijden scherpe snelle de en scharen blaadjes auto's rondjes

58. Luie tieners dekken tafels en de dikke dames brengen koffie.
(Lazy teenagers set tables and the fat ladies bring coffee.)
Reie teezers lenken mabels en de wokke lapes brargen wiffie.
tieners tafels dames koffie de en dekken brengen luie dikke

59. Zure bessen maken vlekken en de zachte bijen maken honing.

(Sour berries make stains and the soft bees make honey.)
Nume betjen lasen zwokken en de nochte guien lapen moping.
maken maken zure zachte de en bessen bijen vlekken honing

60. Vieze mannen smeren olie en de toffe ouders kopen kaartjes.
(Dirty men smear oil and the cool parents buy tickets.)
Bieve wanzen fleven oree en de piffe amders homen koostjes.
mannen olie ouders kaartjes de en smeren kopen vieze toffe

61. Franse schilders verven muren en de Vlaamse bakkers kneden brooddeeg.
(French painters paint walls and the Flemish bakers were kneading bread dough.)
Flanje schunders bernen lunen en de knuimse garkers dreten slooddieg.
verven kneden Franse Vlaamse de en schilders muren bakkers brooddeeg

62. Vlotte lopers maken meters en de boze tieners slopen ruiten.
(Fast runners make meters and the angry teenagers demolish windows.)
Snette rogeres dapen peders en de vone teezers spomen hieten.
lopers meters tieners ruiten de en maken slopen vlotte boze

63. Gele bloemen lokken bijen en de brakke mensen drinken water.
(Yellow flowers attract bees and the hungover people drink water.)
Bese drijmen lunken veien en de plokke moksen plinsen rates.
drinken lokken gele brakke de en bloemen bijen mensen water

64. Zware tassen breken ruggen en de natte sokken brengen blaren.
(Heavy bags break backs and the wet socks cause blisters.)
Plane pansen flesen ruflen en de zaste sunken spelgen spalen.
tassen ruggen sokken blaren de en breken brengen zware natte

65. Losse spijkers sieren muren en de bange muizen graven hollen.
(Loose nails adorn walls and the scared mice dig holes.)
Lunse kloekers suinen luven en de garge mienen slazen mellen.
sieren graven losse bange de en spijkers muren muizen hollen

66. Dronken rappers lopen blauwtjes en de bolle katten aten brokjes.
(Drunk rappers are turned down and the fluffy cats ate kibble.)

Plorken lippers women bleuntjes en de galle mitten uken slekjes.
lopen aten dronken bolle de en rappers blauwtjes katten brokjes

67. Knappe ridders redden levens en de grote paarden winnen prijsjes.
(Handsome knights save lives and the big horses win prizes.)
Flippe ludders hefden rezens en de spode deurden dinzen proekjes.
ridders paarden prijsjes levens de en redden winnen knappe grote

68. Kille zussen stelen spullen en de woeste ouders straffen broertjes.
(Cold sisters steal things and the savage parents punish brothers.)
Wulle zetsen speven krillen en de deuste agders stropfen brooltjes.
stelen straffen kille woeste de en zussen spullen ouders kindjes

69. Slome slakken aten sprietjes en de valse hommels steken kindjes.
(Slow snails ate grass blades and the false bumblebees sting children.)
Ploge spikken osen sproekjes en de vikse lompels speven wirtjes.
slakken sprietjes hommels kindjes de en aten steken slome valse

70. Rotte appels brengen ziektes en de gulle fietsers zingen liedjes.
(Rotten apples bring diseases and the generous cyclists sing songs.)
Hatte ammels spelgen nientes en de gumpe feunsers zansen riegjes.
brengen zingen rotte gulle de en appels ziektes fietsers liedjes

71. Gekke buren maken worstjes en de dikke neven snoepen taarten.
(Crazy neighbors make sausages and the heavy cousins snack on cake.)
Gelse gulen dapen wuchtjes en de mekke zeben smijpen tijnten.
snoepen maken gekke dikke de en buren worstjes neven taarten

72. Dunne meisjes drinken sapjes en de witte duiven aten bonen.
(Thin girls drink juices and the white pigeons ate beans.)
Durre muipjes plinsen sutjes en de kette wuizen uken goven.
meisjes sapjes duiven bonen de en drinken aten witte dunne

73. Knappe mannen strikken veters en de kleine muizen horen piepjes.
(Handsome men tie laces and the little mice heard beeps.)
Flippe wanzen strissen getels en de spiene mieven rolen peugjes.
strikken horen knappe kleine de en mannen muizen veters piepjes

74. Vieze messen snijden appels en de snelle jongens gooien ballen.
(Dirty knives cut apples and the fast guys throw balls.)
Beize letsen floeden ammels en de flolle jargens goenen garlen.
messen appels jongens ballen de en snijden gooien vieze snelle

75. Trage mensen kopen broden en de mooie vrouwen bakken taarten.
(Slow people buy bread and the beautiful women baked pies.)
Klame helsen lomen droten en de moere smouven galken peurten.
kopen bakken trage mooie de en mensen broden vrouwen taarten

76. Luie honden ruiken voedsel en de warme broodjes hebben pitjes.
(Lazy dogs smell food and the hot sandwiches contain seeds.)
Reue rorden hieken baadsel en de marle braagjes rabben pekjes.
voedsel honden broodjes pitjes de en ruiken hebben luie warme

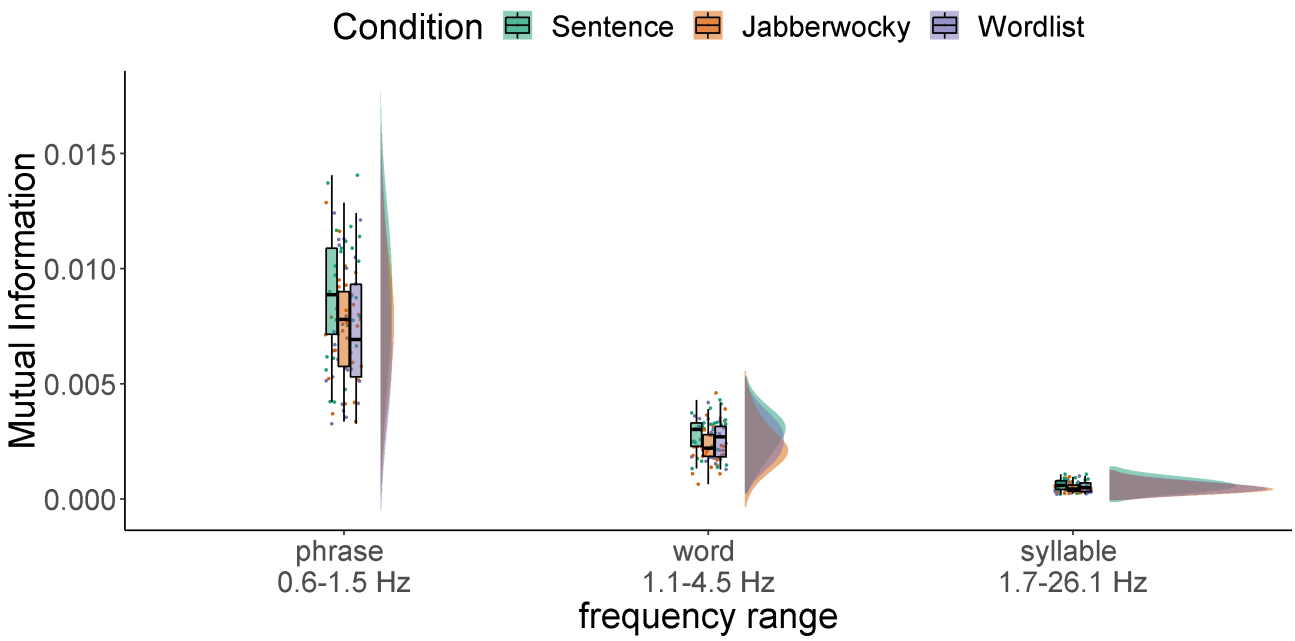
77. Boze ouders geven straffen en de rode vossen graven kuilen.
(Angry parents give punishments and the red foxes dig pits.)
Vome adkers besen strinfen en de lote gussen brazen mielen.
geven graven boze rode de en ouders vossen kuilen straffen

78. Lieve meiden schrijven boeken en de lichte kamers hebben ramen.
(Sweet girls write books and the bright rooms have windows.)
Reive kieden schroezen vijken en de rachte lapers mabben dapen.
meiden boeken kamers ramen de en schrijven hebben lieve lichte

79. Gouden munten hebben waarde en de vreemde vogels fluiten liedjes.
(Golden coins have value and the strange birds whistle songs.)
Gudden kurten rabben laalde en de floemde govels vrieten leugjes.
hebben fluiten gouden vreemde de en munten waarde vogels liedjes

80. Slome treinen hebben stoelen en de rijke boeren voeden koeien.
(Slow trains have seats and the rich farmers feed cows.)
treinen stoelen boeren koeien de en hebben voeden slome rijke
Ploge pleenen labben stijren en de loeke goelen vuiten woenen.

Supplementary Figures



Supplementary Figure A. Phase MI between speech signal and brain response for wider frequency bins. Frequency bins were calculated based on maximum and minimum durations (across all stimuli and conditions) for phrases, words, and syllables (phrases: 0.6-1.5 Hz; words: 1.1-4.5 Hz; syllables: 1.7-26.1 Hz). Note that bins overlap because, naturalistically, durations of linguistic units overlapped. MI was calculated over the entire head. Differences between Sentence – Jabberwocky and Sentence – Wordlist were significant on the phrase and syllable timescale; between Sentence – Wordlist on the word timescale. No significant differences were found for the backward conditions.

Tables.

Table 1a. Mixed-effects logistic regression results for log-transformed, trimmed phase MI in the phrase frequency band. [a] Contrast coded (treatment coding with Sentence as reference level); [b]Contrast coded (treatment coding with Forward as reference level).

	Estimate	SE	df	t	*p*	Variance	SD
Fixed effects							
Intercept	-4.421	0.086	29.473	-51.433	< 0.01		
Condition[T.Jabberwocky][a]	-0.497	0.097	29.411	-5.139	< 0.01		
Condition[T.Wordlist][a]	-0.402	0.117	29.369	-3.421	< 0.01		
Direction[T.Backward][b]	-0.805	0.106	29.731	-7.626	< 0.01		
Condition:Direction [T.Jabberwocky]:[T.Backward]	0.368	0.150	29.086	2.455	0.02		
Condition:Direction [T.Wordlist]:[T.Backward]	0.336	0.168	29.099	2.011	0.06		
Random effects							
Intercept | Participant						0.170	0.412
Condition[T.Jabberwocky][a] | Participant						0.187	0.431
Condition[T.Wordlist][a] | Participant						0.315	0.561
Direction[T.Backward][b] | Participant						0.236	0.486
Condition[T.Jabberwocky][a]:Direction[T.Backward] [b] | Participant						0.479	0.692
Condition[T.Wordlist] [a]:Direction[T.Backward] [b] | Participant						0.646	0.804

Table 1b. Pair-wise contrast results for log-transformed, trimmed phase MI per Direction in the phrase frequency band.

	Estimate	SE	df	t	*p*
Forward					
Sentence – Jabberwocky	0.497	0.099	29.97	5.049	< 0.01
Sentence – Wordlist	0.402	0.120	29.99	3.361	< 0.01
Jabberwocky – Wordlist	-0.096	0.103	30.09	-0.929	0.63

Backward					
Sentence – Jabberwocky	0.130	0.122	30.00	1.060	0.55
Sentence – Wordlist	0.066	0.130	30.02	0.509	0.87
Jabberwocky – Wordlist	-0.063	0.135	30.02	-0.470	0.89

Table 2a. Mixed-effects logistic regression results for log-transformed, trimmed phase MI in the word frequency band. [a] Contrast coded (treatment coding with Sentence as reference level); [b]Contrast coded (treatment coding with Forward as reference level).

	Estimate	SE	df	t	*p*	Variance	SD
Fixed effects							
Intercept	-5.322	0.767	28.437	-69.359	< 0.01		
Condition[T.Jabberwocky][a]	-0.380	0.121	28.790	-3.143	< 0.01		
Condition[T.Wordlist][a]	-0.120	0.072	30.047	-1.666	0.11		
Direction[T.Backward][b]	-0.474	0.126	29.034	-3.754	< 0.01		
Condition:Direction [T.Jabberwocky]:[T.Backward]	0.174	0.176	29.124	0.989	0.33		
Condition:Direction [T.Wordlist]:[T.Backward]	0.057	0.142	29.074	0.404	0.69		
Random effects							
Intercept | Participant						0.127	0.357
Condition[T.Jabberwocky][a] | Participant						0.338	0.581
Condition[T.Wordlist][a] | Participant						0.063	0.250
Direction[T.Backward][b] | Participant						0.378	0.615
Condition[T.Jabberwocky]:Direction[T.Backward] | Participant						0.726	0.852
Condition[T.Wordlist]:Direction[T.Backward] | Participant						0.412	0.642

Table 2b. Pair-wise contrast results for log-transformed, trimmed phase MI per Direction in the word frequency band.

	Estimate	SE	df	t	*p*
Forward					
Sentence – Jabberwocky	0.380	0.123	30.05	3.086	0.01
Sentence – Wordlist	0.120	0.073	29.72	1.633	0.25
Jabberwocky – Wordlist	-0.260	0.140	30.07	-1.858	0.17
Backward					
Sentence – Jabberwocky	0.206	0.119	30.02	0.536	0.85
Sentence – Wordlist	0.062	0.117	30.02	0.536	0.854
Jabberwocky – Wordlist	-0.144	0.102	30.04	-1.415	0.35

Table 3a. Mixed-effects logistic regression results for log-transformed, trimmed phase MI in the syllable frequency band. [a] Contrast coded (treatment coding with Sentence as reference level); [b]Contrast coded (treatment coding with Forward as reference level).

	Estimate	SE	df	t	*p*	Variance	SD
Fixed effects							
Intercept	-6.451	0.082	26.882	-78.910	< 0.01		
Condition[T.Jabberwocky][a]	0.073	0.093	28.886	0.790	0.44		
Condition[T.Wordlist][a]	0.074	0.111	29.265	0.664	0.51		
Direction[T.Backward][b]	-0.003	0.094	27.198	-0.034	0.97		
Condition:Direction [T.Jabberwocky]:[T.Backward]	0.061	0.142	29.188	0.429	0.67		
Condition:Direction [T.Wordlist]:[T.Backward]	0.079	0.159	28.395	0.533	0.60		
Random effects							
Intercept | Participant						0.149	0.387
Condition[T.Jabberwocky][a] | Participant						0.161	0.401
Condition[T.Wordlist][a] | Participant						0.271	0.521
Direction[T.Backward][b] | Participant						0.168	0.410
Condition[T.Jabberwocky]:Direction[T.Backward] | Participant						0.410	0.640
Condition[T.Wordlist]:Direction[T.Backward] | Participant						0.466	0.683

Table 3b. Pair-wise contrast results for log-transformed, trimmed phase MI per Direction in the syllable frequency band.

	Estimate	SE	df	t	*p*
Forward					
Sentence – Jabberwocky	-0.073	0.944	29.97	-0.775	0.72
Sentence – Wordlist	-0.074	0.113	30.11	-0.651	0.79
Jabberwocky – Wordlist	-0.001	0.105	30.05	-0.006	1.0
Backward					
Sentence – Jabberwocky	-0.134	0.110	30.02	-1.215	0.45
Sentence – Wordlist	-0.153	0.096	29.97	-1.591	0.27
Jabberwocky – Wordlist	-0.019	0.132	30.04	-0.143	0.99

Table 4a. Mixed-effects logistic regression results for log-transformed, trimmed phase MI between brain and dimensionality-reduced stimuli. [a] Contrast coded (treatment coding with Sentence as reference level); [b]Contrast coded (treatment coding with Forward as reference level).

	Estimate	SE	df	t	*p*	Variance	SD
Fixed effects							
Intercept	-5.977	0.076	25.757	-78.813	< 0.01		
Condition[T.Jabberwocky][a]	-0.328	0.095	29.219	-3.436	< 0.01		
Condition[T.Wordlist][a]	-0.522	0.110	27.529	-4.737	< 0.01		
Direction[T.Backward][b]	-0.685	0.112	25.071	-6.135	< 0.01		
Condition:Direction [T.Jabberwocky]:[T.Backward]	0.254	0.156	28.115	1.627	0.11		
Condition:Direction [T.Wordlist]:[T.Backward]	0.580	0.154	28.464	3.785	< 0.01		
Random effects							
Intercept | Participant						0.130	0.360
Condition[T.Jabberwocky] | Participant						0.195	0.441
Condition[T.Wordlist] | Participant						0.283	0.532
Direction[T.Backward] | Participant						0.291	0.540
Condition[T.Jabberwocky]:Direction[T.Backward] | Participant						0.572	0.756
Condition[T.Wordlist]:Direction[T.Backward] | Participant						0.555	0.745

Table 4b. Pair-wise contrast results for log-transformed, trimmed phase MI between brain and dimensionality-reduced stimuli.

	Estimate	SE	df	t	*p*
Forward					
Sentence – Jabberwocky	0.0.328	0.097	29.95	3.371	< 0.01
Sentence – Wordlist	0.522	0.113	30.15	4.643	< 0.01
Jabberwocky – Wordlist	0.194	0.114	30.07	1.707	0.22
Backward					
Sentence – Jabberwocky	0.074	0.106	30.05	0.694	0.77
Sentence – Wordlist	-0.058	0.094	30.06	-0.618	0.81
Jabberwocky – Wordlist	-0.132	0.104	30.05	-1.262	0.43