Lexical frequency and sentence context influence the brain's response to single words

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Abstract

Remarkably fast reading is facilitated by brain processes that are sensitive to both word frequency and contextual constraints. It is debated as to whether these attributes have additive or interactive effects on language processing in the brain. We investigated this issue by analysing existing magnetoencephalography data from 99 participants reading *sentences* and *word-lists.* Using a cross-validated model comparison scheme, we found that lexical frequency predicted the word-by-word elicited MEG signal in a widespread cortical network, irrespective of sentential context. In contrast, index (ordinal word position) was more strongly encoded in sentence words, in left front-temporal areas. This suggests that frequency influences word processing independently of predictability, and that contextual constraints affect word-by-word brain responses. Interestingly, an exploration of the index*frequency interaction revealed an effect (in left frontal and temporal cortex) that reversed in time and space for sentences compared to word-lists. These findings may improve future neuro-cognitive models of reading.

Keywords: sentence reading, lexical frequency, prediction, context, magnetoencephalography, hyperalignment.

1. Introduction

When reading a text, the reader's brain is capable of rapidly extracting meaning from the structured sequence of individual words. In order to achieve its remarkable efficiency in processing, the brain network for language not only extracts, and actively uses, lexical properties of the individual words, but is also greatly influenced by the context in which those words occur. On the one hand, for instance, words that maintain a highly frequent occurrence in day-to-day language use are processed faster and with less effort than words that occur less frequently (Calvo & Meseguer, 2002; Inhoff & Rayner, 1986; Rayner & Duffy, 1986; Rubenstein, Garfield, & Millikan, 1970). On the other hand, as a linguistic expression unfolds, the previously read input provides the brain with a constraining semantic and syntactic context, which may allow for predictions to be made about the upcoming word. This results in measurable effects at fast timescales, in response times (Staub, Grant, Astheimer, & Cohen, 2015), and in both electrophysiological (Van Petten & Kutas, 1990) and eye movement signals (Calvo & Meseguer, 2002).

Typical adult readers effortlessly process an average of 238 words per minute (Brysbaert, 2019), fixating on each word for an average of only 235ms (Rayner, 1986). The brain's rapid word processing has been shown to be facilitated when the word frequently occurs within a given language (i.e. has a high *lexical frequency*). Compared to low frequency words, high frequency words are fixated for shorter durations during reading (Calvo & Meseguer, 2002; Inhoff & Rayner, 1986; Rayner & Duffy, 1986), are responded to faster in lexical decision tasks (Rubenstein et al., 1970), and produce smaller electrophysiological (Smith & Halgren, 1987; Van Petten & Kutas, 1990) and hemodynamic responses (Chee, Hon, Caplan, Lee, & Goh, 2002). It seems therefore that processing of high frequency words is less effortful than low frequency words.

The prediction of upcoming sentential content is another mechanism that seems to facilitate the remarkable speed of sentence reading. There is now ample evidence that one is able to predict upcoming linguistic input, although whether this is to the level of semantics, syntactic content or the word form is still debated (Pickering & Gambi, 2018). Regardless of the level at which prediction takes place, highly predictable words seem to be processed faster than unpredictable words, reflected in shorter fixation durations (Calvo & Meseguer, 2002; Rayner & Well, 1996) and smaller N400 responses (Van Petten & Kutas, 1990). The N400 is an electrophysiological marker of semantic processing and unification, occurring between 200-600ms at a centro-parietal topography (Hagoort, Baggio, & Willems, 2009; Kutas & Federmeier, 2011). A larger N400 response is observed when the integration of semantic information is more difficult, for example when the word is less predictable.

There is increasing agreement that there are two mechanisms through which prediction can take place. Firstly, through a fast, effortless and automatic mechanism, in which activity spreads to associated features,

or, secondly, through an “active reasoning” mechanism, in which world knowledge and the surrounding context are combined to form predictions (Huettig, 2015; Pickering & Gambi, 2018). Lexical frequency could therefore influence the automatic, bottom-up prediction mechanism, where activation thresholds are lower for high compared to low frequency words. In contrast, effects of the semantic and syntactic constraints, provided by the context that a word is presented in, may reflect a prediction mechanism that relies on the top-down flow of information from strong priors. For example, as semantic context increases as the sentence unfolds a stronger foundation on which to base predictions is provided. In this study, we follow earlier approaches in using ordinal word position in a sentence (or *index*) to roughly quantify context. Indeed, the N400 has been shown to decrease with both increased lexical frequency and increased index (Dambacher, Kliegl, Hofmann, & Jacobs, 2006; Payne, Lee, & Federmeier, 2015; Van Petten & Kutas, 1990), which suggests that word integration becomes easier as each of these factors increase.

A recurring finding in the literature is that there is an interaction between effects of increased predictability and lexical frequency on the N400, where the effect of word frequency on the N400 amplitude during word processing is greatly diminished or disappears with increased context or predictability (Alday, Schlesewsky, & Bornkessel-Schlesewsky, 2017; Dambacher et al., 2006; Payne et al., 2015; Sereno, Hand, Shahid, Mackenzie, & Leuthold, 2019; Van Petten & Kutas, 1990). Similar interactions have also been observed at earlier time windows (Dambacher et al., 2012; Sereno, Brewer, & O'Donnell, 2003; Sereno et al., 2019) and with functional near-infrared spectroscopy (fNIRS; Hofmann et al., 2014). This has lead authors to conclude that lexical frequency merely reflects a bottom-up, baseline level of expectation that is soon overridden with top-down information in the presence of context (Kretzschmar, Schlesewsky, & Staub, 2015).

However, there is a well-documented discrepancy between the aforementioned electrophysiological literature and the eye-tracking literature as to whether frequency and predictability indeed have an interactive effect on word processing, or whether effects are additive (Kretzschmar et al., 2015). In contrast to the findings of the N400 literature, recording participants’ eye gaze during reading has consistently demonstrated an additive effect of lexical frequency and predictability on fixation durations. Fixation durations are longer for highly predictable low frequency words than highly predictable high frequency words, and again longer for unpredictable low frequency words (Kennedy, Pynte, Murray, & Paul, 2013; Kretzschmar et al., 2015; Staub, 2015; Staub & Benatar, 2013). One explanation for these contradictory findings is that lexical frequency and prediction have separate additive effects during early processing stages (Sereno et al., 2019; Staub & Goddard, 2019), for example during orthographic processing or lexical retrieval, but that frequency effects are not present with increased context during later semantic processing and integration.

1.1. The current work

Considering the aforementioned ambiguity in the theoretical understanding of how lexical frequency influences subsequent processing, specifically in the light of additional context-based predictability, the current work performed a novel analysis on an existing dataset, with the aim to dissociate lexical frequency effects from predictability effects. Although previous work has sought to define *when* frequency and predictability interact, less attention has been invested into examining the spatiotemporal dynamics of this interaction. Moreover, Staub and Goddard (2019) recently highlighted that current models of word reading, such as the E-Z reader (Reichle, Rayner, & Pollatsek, 2003) and SWIFT (Engbert, Nuthmann, Richter, & Kliegl, 2005), do not yet completely account for effects of predictability and invalid previews on fixation durations. Considering the complex effects lexical attributes have on the neural processing of language, a comprehensive account of word reading could benefit from improving upon both the temporal and spatial resolution of previous work.

Specifically, we used the Mother of all Unification Studies (MOUS; Schoffelen et al., 2019), a large sample size open-access dataset of 102 participants in which magnetoencephalography (MEG) was recorded while they read sentences and scrambled sentences (word-lists). Improving upon previous electroencephalography (EEG), functional magnetic resonance imaging (fMRI) and fNIRS research, MEG provides both the temporal and spatial resolution to detect subtle and fine-grained differences in the extent that lexical frequency and predictability are encoded in the MEG signal after word-onset, which could have previously been lost by averaging over time and space. With respect to the analysis, and in contrast to most previous work, we exploited the word-by-word variability in the MEG signal, which is often lost through averaging across words of the same experimental condition. Specifically, we used multiset canonical correlation analysis (MCCA) to boost the stimulus-specific signal (Arana, Marquand, Hultén, Hagoort, & Schoffelen, 2020), and performed detailed cross-validated single-trial encoding model analysis, using regression models that quantified the degree to which lexical frequency and various measures of predictability are encoded in the MEG signal.

2. <u>Methods</u>

2.1. Participants

Participants were 99 right-handed native Dutch speakers (age range 18-33 years; mean age = 22; 50 males) from a subset of 102 participants who completed a reading paradigm in the open-access MOUS dataset (Mother of all Unification Studies; Schoffelen et al., 2019). Three participants were excluded from analyses, due to technical issues during data acquisition making them unsuitable for the current analysis pipeline. All participants were right handed, had normal or corrected to normal vision, and reported no history of

neurological, developmental or language impairments. All participants provided written informed consent and the study was approved by the local ethics committee, and complied with the declaration of Helsinki.

2.2. Sentence stimuli

The total stimulus set consisted of 360 Dutch sentences (9-15 words in length), which are described in detail in Schoffelen et al. (2019). Each participant read a selection of 240 sentences (2/3 of the entire stimulus set), where 50% were presented as intact sentences and 50% were presented as scrambled sentences (henceforth referred to as *word-lists).* Specifically, three pairs of selections, referred to as *scenario pairs*, were created, such that the stimuli that occurred as normal sentences in one scenario from a pair were presented in a scrambled fashion in the other scenario from that pair, and vice versa. No participant read both the intact and scrambled version of a sentence. Consequently of this design was that the collection of words that subjects read was exactly counterbalanced across sentence and word-list conditions, both across all participants and within the three sets of scenario pairs.

2.3. Lexical characteristics

Lexical characteristics of frequency, index, surprisal, entropy and length (i.e. number of characters) were obtained for each word in the sentence, to enter as predictors into regression models. *Lexical frequency* was defined as the frequencies of words occurring in the NLCOW2012 corpus (Schäfer & Bildhauer, 2012) and were log10 transformed. The NLCOW2012 database is comprised of over 10 million Dutch sentences (71761868 words), and was also used to obtain estimates of surprisal and entropy (see below). *Index* was defined as the ordinal position of the word in the sentence/word-list. Each word's *surprisal* value was acquired from a trained tri-gram model, using WOPR (http://ilk.uvt.nl/wopr/), trained on the NLCOW2012 corpus. Surprisal was computed as the log10 transform of perplexity, and reflects how surprising the word was, given the previous two words in the sentence. High surprisal signifies low word predictability. *Entropy* was acquired from the same trained tri-gram model. Entropy reflects the probability distribution of possible continuations, given the constraints of the previous three words. High entropy values signify a high number of possible continuations, i.e. low predictability of the upcoming word.

2.4. Experimental procedure

Sentence/word-list stimuli were presented in a random order in alternating sentence and word-list blocks. There were 48 blocks in total, each containing five sentences or five word-lists. The starting block condition (sentence/word-list) was randomised across participants. At the beginning of each block the block type was presented on the screen for 1500ms. Trials (sentences/word-lists) were separated with a 3200-4200ms inter-trial interval, during which a blank screen was presented followed by a fixation cross. Stimuli were presented word-by-word, with an inter-stimulus (word) interval of 300ms. The presentation duration of

each word was adjusted by the word duration when spoken (300-1400ms, mean = 351ms; see Schoffelen et al., 2019).

Participants were instructed to read the sentences. On 20% of trials participants answered a yes/no comprehension question to ensure they were engaged in the task. The positions of the comprehension questions relative to the stimuli were random. In sentence blocks, 50% of questions asked about the content of the sentence (e.g. "Did grandma give a cookie to the girl?"). Questions in the word-list blocks, and the remaining 50% of questions in the sentence blocks, asked about the presence of a content word (e.g. "Was the word *grandma* mentioned?"). Participants responded to the questions by pressing a button with their left index/middle finger to answer yes/no, respectively.

Stimuli were presented with Presentation software (Version 16.0, Neurobehavioral Systems, Inc) and back-projected with an LCD projector at a refresh rate of 60Hz. Words were presented in the centre of the screen in a black mono-spaced font (visual angle of 4 degrees) on a grey background. Before beginning the main experiment, participants completed practice trials to familiarise themselves with the procedure.

2.5. MEG acquisition

Participants were seated in a magnetically shielded room, while MEG was recorded with a 275 axial gradiometer CTF system, at a sampling rate of 1200 Hz and with a 300 Hz analog low pass filter. Prior to the recording, the participant's head shape was digitised with a Polhemus 3D-Space Fast-track digitiser. Digitised head shapes and fiducial points were later used to coregister subject-specific anatomical MRIs with the MEG sensor space. The position of the participants' head (relative to the MEG sensors) was monitored online throughout the recording via three head-localiser coils, placed on the nasion and left and right pre-auricular points.

2.6. MRI acquisition

MRIs were recorded with a Siemens Trio 3T MRI scanner with a 32-channel head coil. A T1-weighted magnetisation-prepared rapid acquisition gradient echo pulse sequence was used to obtain structural MRIs (volume TR = 2300ms; TE = 3.03ms; 8° flip angle; 1 slab; slice matrix size = 256 × 256; slice thickness = 1mm; field of view = 256mm; isotropic voxel size = 1.0 × 1.0 × 1.0mm). A vitamin E capsule was placed behind the right ear as a fiducial marker to visually identify left/right.

2.7. Data analysis

Pre-processing

Data were band pass filtered between 1-20Hz and epoched time-locked to sentence onset. Segments of data that contained eye blinks, squid jumps and muscle artifacts were replaced with "Not a Number" (NaN) in order to preserve the original sentence onset related timing information. Data were downsampled to 120Hz.

Source Reconstruction

Single shell head models describing the inside of the skull were constructed from individual MRIs, which were used to create forward models according to (Nolte, 2003). Single trial covariance matrices were computed between sensor pairs. Sources were reconstructed using linearly constrained minimum variance (LCMV; Van Veen, van Drongelen, Yuchtman, & Suzuki, 1997) beamforming to obtain time courses of source activity at 8196 dipole locations. Data were parcellated using an anatomical atlas-based parcellation, consisting of 382 parcels (Schoffelen et al., 2017). For each parcel, principal component analysis was performed on the dipole time series belonging to a given parcel, and the top five components that explained the most variance in the parcel-specific signal were selected for further analysis.

Spatiotemporal Alignment

To boost the stimulus specific signal, and reduce intersubject variability, data were spatiotemporally aligned across subjects using multiset canonical correlation analysis (MCCA; Arana et al., 2020). MCCA was performed separately for each pair of scenarios, which were matched in terms of the stimulus material that was used to derive the sentences and the word-lists (i.e. the subjects read exactly the same overall collection of individual words), based on combining data from sets of 32-34 subjects. Time series (time-locked to stimulus onsets) were shifted in time from -50-50ms in steps of single samples, resulting in 65 time series per word per parcel (i.e. 5 principal components × 13 time shifts), to account for potential response latency differences across subjects. Next, the time series of the word-list trials were unscrambled such that the word order matched the corresponding sentence's word order. The resulting time series were entered into a five-fold cross validated MCCA to maximise the intersubject correlation. The basic MCCA procedure has been described in detail by Arana et al. (2020). To summarise, MCCA was used to find linear combinations of the 65 parcel time courses (canonical components) that maximised the correlation between all subject pairs, while they were presented with exactly the same words, thereby increasing the similarities between the participants' signals in response to those words.

Encoding Models

Next, we fitted encoding models to the data, using five-fold cross-validated ridge regression. To this end, the subject-specific canonical components were re-epoched time-locked to word onset, selecting only content words (nouns, adjectives, and verbs). For these re-epoched data, subject-specific encoding models were estimated for each time point and parcel-of-interest, separately for sentence and word-list words. The optimal regularisation parameter was estimated using nested cross-validation, and selected from a range of values (0.002, 0.005, 0.010, 0.020, 0.050, 0.100, 0.200, 0.500, 1.000, 2.000 and 5.000) for each model.

We used a model comparison scheme to quantify the extent to which a model including a predictor of interest explained variance in the MEG signal, above and beyond a reduced model that did not include the given predictor. To this end we computed the coefficient of determination:

$$R^2 = 1 - \frac{\sum(y - \hat{y}_{full\ model})^2}{\sum(y - \hat{y}_{reduced\ model})^2}$$

Where the numerator and denominator in the right side of the equation were computed as the sum-of-squares of the difference between the data and the modelled test data, for the full and reduced models, respectively.

To test the contribution of individual predictors we used a full model that included, beyond a constant and word length, the following predictors of interest: lexical frequency (log transformed), surprisal, entropy and index. To test the interaction between lexical frequency and context – as quantified with index (similar to Alday et al., 2017; Payne et al., 2015; Van Petten & Kutas, 1990) – we used a full model that included only, beyond a constant, the individual predictors of lexical frequency (log transformed), index, and the interaction term, which was computed as an element wise product: lexical frequency (log10 transformed) × index.

Epochs (content words) were divided into five equal folds to avoid overfitting, and to allow for the generalisation across items. For each fold of the cross-validation procedure, the model was estimated using data from the four other folds, and tested on the remaining data.

In order to be able to statistically compare the models for the individual sentence and word-list conditions, that is to obtain an estimate of a possible bias in the coefficient of determination under the null hypothesis, we used a permutation approach, as follows: For each model, the design matrix was randomly permuted 50 times and, for each permutation, an additional model was trained and tested with the permuted variables, thereby removing any true association between the predictors and the data.

Statistical Analysis

We statistically evaluated the individual predictors in a selection of regions-of-interest (ROI), consisting of 184 parcels (92 left hemisphere parcels with their right hemisphere counterparts). This selection consisted of cortical regions that have consistently been described to be a part of a language network (Catani et al., 2007; Friederici, 2009; Glasser & Rilling, 2008; Schoffelen et al., 2017) or to be involved in the processing of semantic relationships (Bunge, Helskog, & Wendelken, 2009; Frankland & Greene, 2020; Knowlton, Morrison, Hummel, & Holyoak, 2012; Ramnani & Owen, 2004). We further investigated the interaction between lexical frequency and index based on the resulting map including only the 33 parcels which significantly encoded index or lexical frequency.

We used non-parametric permutation statistics, using the dependent samples T-statistic across subjects as a test statistic. We evaluated the individual coefficients of determination against the corresponding average of their 50 random permutation counterparts (see Encoding Models section 2.7), using an alpha-level of 0.05 for inference. The sentence and word-list conditions were compared with each other using a two-sided test (which involves evaluating the test statistic against two randomisation distributions, using an alpha level of 0.025 for each of these randomisation distributions) for inference. For all comparisons, multiple comparisons (across time and space) were accounted for by using a max-statistic distribution from 5000 permutations.

3. Results

All participants achieved over 60% accuracy on the comprehension questions (mean = 81.19%; sd = 6.61%), confirming they were attending to the stimuli. No further analysis was conducted on the comprehension questions.

3.1. Spatiotemporal Alignment

Figure 1 shows the effect of the alignment procedure, presenting the time-resolved intersubject correlation (Fisher Z-transformed correlation coefficient) after spatiotemporal alignment (solid green line), spatial alignment (dashed green line), temporal alignment (dotted red line) and no alignment (dashed purple line), for two example parcels (sub-regions of BA22 and BA44). Figure 1 illustrates that spatiotemporal alignment increased the intersubject correlation, more so than temporal alignment alone or spatial alignment alone. The intersubject correlation peaked at around 400ms (300-500ms), a time period in which electrophysiological brain signal is typically found to be influenced by the semantic characteristics of a word (N400/M400; Kutas & Federmeier, 2011). Spatiotemporal alignment thereby seems to have boosted the stimulus specific signal in the data.

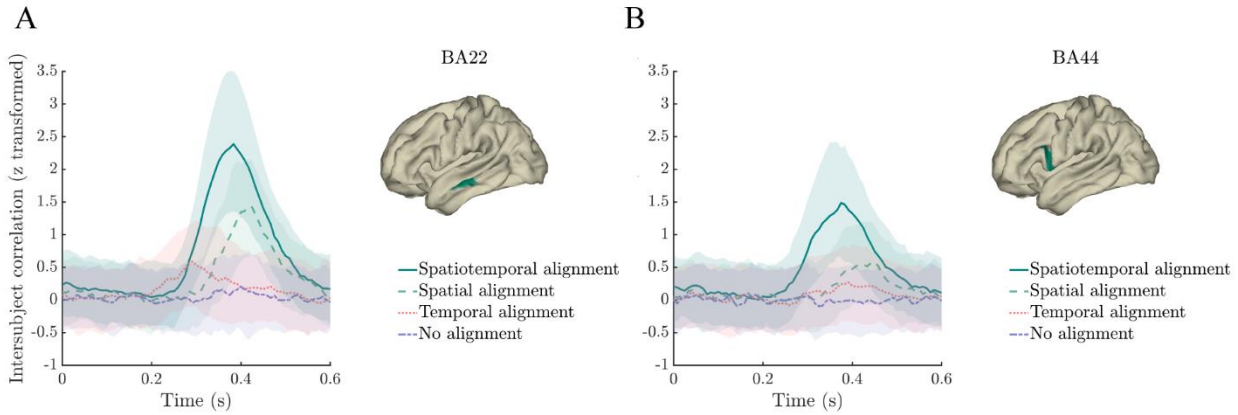

Figure 1. MCCA boosts intersubject consistency of single word responses. Time courses of Z-transformed intersubject correlations after spatiotemporal alignment (solid green line), spatial alignment (dashed green line), temporal alignment (dotted red line) and no alignment (dashed purple line) in middle temporal gyrus (parcel in Brodmann Area (BA) 22; panel A) and inferior frontal gyrus (parcel in BA44; panel B). Shaded ribbons represent the interquartile range.

3.2. Encoding Models

For each measure of interest, our model comparison scheme quantified the extent that each regressor explained word-specific variance in the MEG signal, beyond the variance explained by all other regressors (see Methods section 2.7). Similarly, we quantified the variance explained by the index × lexical frequency interaction, beyond that explained by the main effects of lexical frequency and index. The model comparisons were statistically evaluated separately for the sentences (Figs 2-6 panel A) and word-lists (Figs 2-6 panel B) against a permutation derived baseline, as well as compared against each other (Figs 2-6 panel C).

Lexical Frequency

Lexical frequency significantly predicted MEG signal in both sentences and word-lists throughout the 0-600ms analysis window (relative to word onset), spatially spreading from bilateral occipital and inferior temporal cortex to left posterior and middle temporal cortex at time points preceding 250ms, to left frontal and left anterior temporal cortex from 250ms onwards. In both sentences and word-lists, the effect of lexical frequency peaked at around 400ms in left temporal and frontal cortex (Fig 2 panels A and B). In the left superior temporal gyrus (STG) and middle temporal gyrus (MTG) this effect started earlier in sentences compared to word-lists, from 183ms, compared to 267ms in lists.

Despite the seemingly stronger effect in word-lists compared to sentences - apparent in the time courses in Fig 2 panel D - in a direct comparison of the coefficient of determination for lexical frequency across conditions (presented in Fig 2 panel C), only a very small spatiotemporal effect survived the multiple comparison correction scheme. Specifically, significantly more variance was explained in sentences

compared to word-lists at a single time point, at 267ms, in a single right hemisphere frontal parcel (BA46). There were no other significant differences between sentences and word-lists in the variance explained by lexical frequency (corrected $p>.05$).

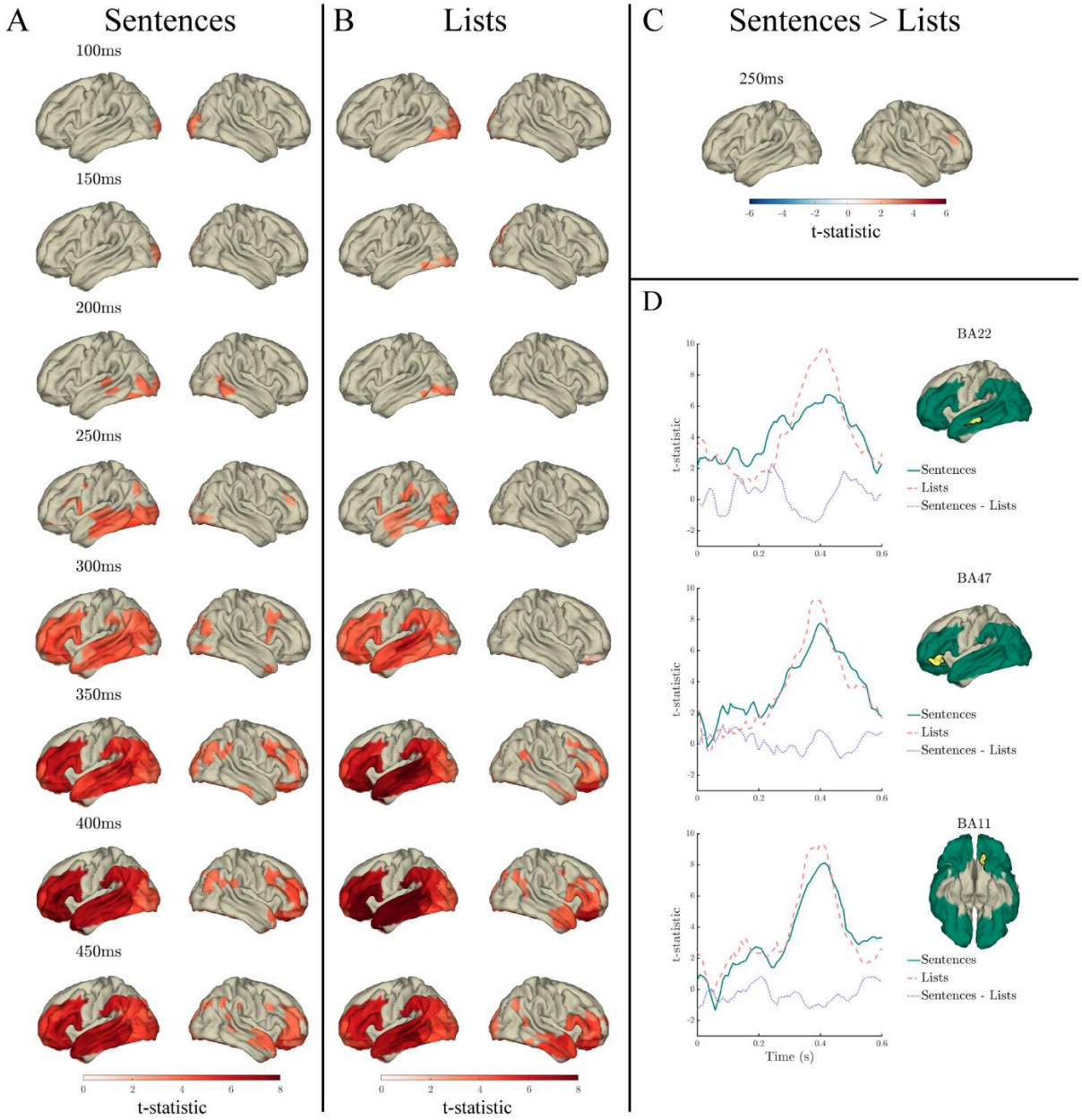

Figure 2. Surface plots of T-statistics (averaged over 50ms time windows centred at the indicated latencies, for visualisation) quantifying the difference in variance explained by lexical frequency (log10 transformed), beyond that explained by index, surprisal, entropy and length, in sentence compared to random permutation models (panel A; $p<.05$ one-sided, corrected), word-list compared to random permutation models (panel B; $p<.05$ one-sided, corrected), and sentence compared to word-list models (panel C; $p<.05$ two-sided, corrected). Parcels for which no time point was significant during the 50ms time bin are masked. Panel D: Time courses of T-statistics for sentence (solid green line) and word-list (dashed red line) models compared to random permutation models, and sentence compared to word-list models (dotted purple line) for subparcels of BA22, BA47 and BA11 (highlighted in yellow on adjacent surface plots). ROIs entered into statistical analyses are illustrated as green shaded area on surface plots.

Index

Index significantly predicted the MEG signal in both sentences and word-lists throughout the 0-600ms analysis window. In sentences the effect spread from bilateral occipital cortex throughout right posterior and inferior temporal cortex and left temporal and frontal cortex, and peaked at around 350ms in left anterior temporal and inferior frontal cortex (Fig 3 panel A). In contrast to sentences, in word-lists the effect was predominantly constrained to bilateral occipital and inferior temporal cortex, peaked at around 300ms in left posterior and inferior temporal cortex (Fig 3 panel B), and after 492ms only two single time points were significant (542ms and 600ms).

Significantly more variance in the MEG signal was predicted by index in sentences compared to word-lists from 275-417ms in anterior temporal (BA21/22/38), 283-375ms in inferior frontal (BA44/46/47), and 258-400ms in orbitofrontal and prefrontal cortex (PFC; BA10/11), as is evident in Fig 3 panel C.

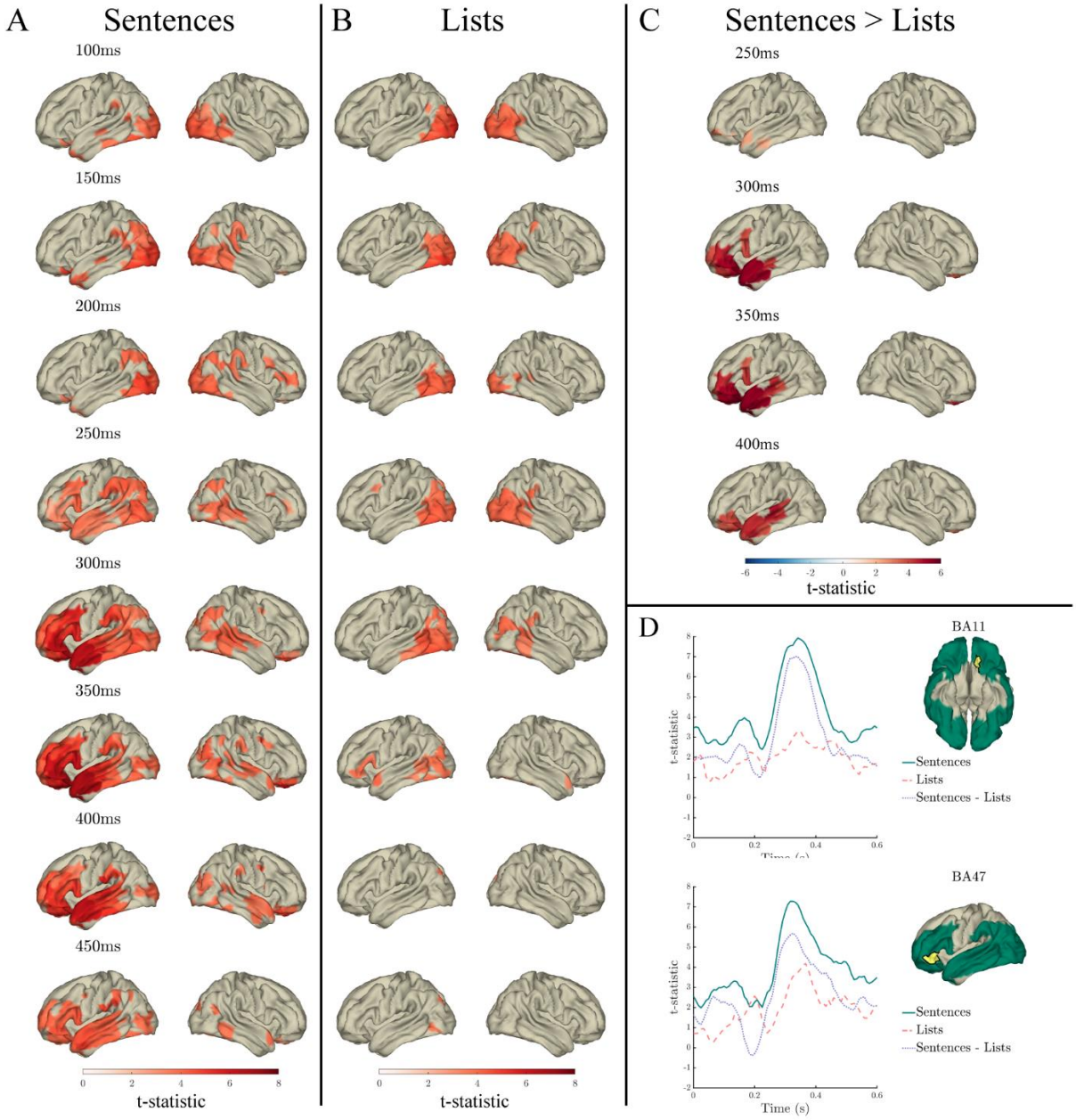

Figure 3. Surface plots of T-statistics (averaged over 50ms time windows centred at the indicated latencies, for visualisation) quantifying the difference in variance explained by index, beyond that explained by lexical frequency (log10 transformed), surprisal, entropy and length, in sentence compared to random permutation models (panel A; $p<.05$ one-sided, corrected), word-list compared to random permutation models (panel B; $p<.05$ one-sided, corrected), and sentence compared to word-list models (panel C; $p<.05$ two-sided, corrected). Parcels for which no time point was significant during the 50ms time bin are masked. Panel D: Time courses of T-statistics for sentence (solid green line) and word-list (dashed red line) models compared to random permutation models, and sentence compared to word-list models (dotted purple line) for subparcels of BA11 and BA47 (highlighted in yellow on adjacent surface plots). ROIs entered into statistical analyses are illustrated as green shaded area on surface plots.

Surprisal

In both sentences and word-lists, surprisal significantly predicted the MEG signal throughout most of the analysis window, peaking at 400ms in temporal and frontal cortex, and predicting additional right hemisphere variance in orbitofrontal and anterior temporal cortex (see Fig 4 panels A and B). In sentences, the effect spread from STG and the angular gyrus from 0-100ms, throughout temporal and frontal cortex from 208-600ms (Fig 4 panel A). In word-lists, the effect spread from left (later bilateral) occipital and inferior temporal cortex throughout primarily the left temporal and frontal cortex (Fig 4 panel B). However, the effect of surprisal in word-lists was most robust from 200ms onwards. Preceding 200ms, only several individual time points were significant after multiple comparisons correction.

Significantly more variance in the MEG signal was predicted by surprisal in sentences compared to word-lists 50-58ms and 458-475ms relative to word onset in left MTG (BA22), and 392-442ms relative to word onset in bilateral orbitofrontal cortex (BA11), which is presented in Fig 4 panel C. The time courses in Fig 4 panel D illustrate that the significant difference in BA22 results from a more sustained response in sentences compared to word-lists, whereas BA11 results from a greater peak in sentences compared to word-lists.

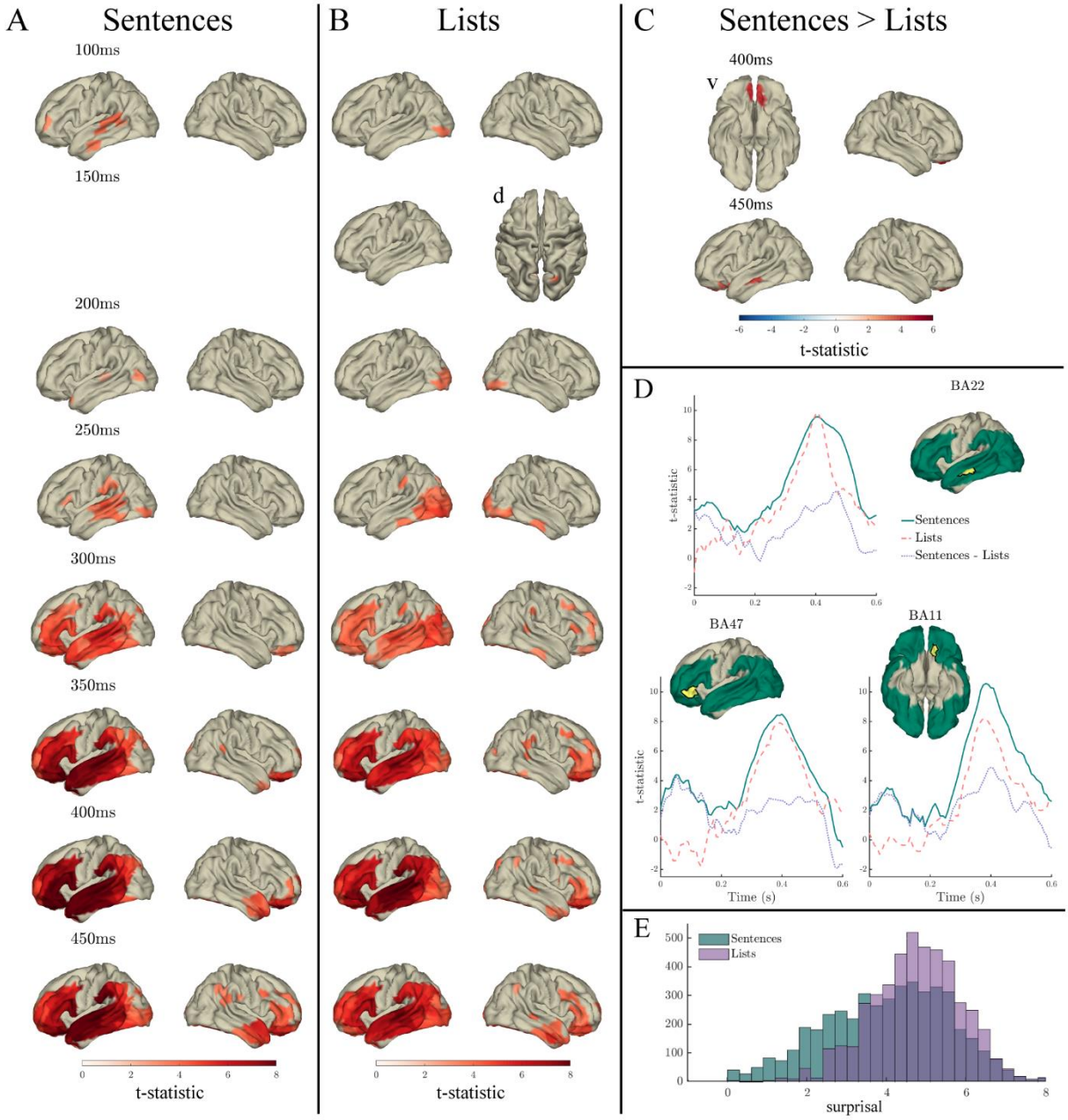

Figure 4. Surface plots of T-statistics (averaged over 50ms time windows centred at the indicated latencies, for visualisation) quantifying the difference in variance explained by surprisal, beyond that explained by lexical frequency (log10 transformed), index, entropy and length, in sentence compared to random permutation models (panel A; $p<.05$ one-sided, corrected), word-list compared to random permutation models (panel B; $p<.05$ one-sided, corrected), and sentence compared to word-list models (panel C; $p<.05$ two-sided, corrected). Parcels for which no time point was significant during the 50ms time bin are masked. Ventral and dorsal views are indicated with adjacent "v" and "d" labels, respectively. Panel D: Time courses of T-statistics for sentence (solid green line) and word-list (dashed red line) models compared to random permutation models, and sentence compared to word-list models (dotted purple line) for subparcels of BA22, BA47 and BA11 (highlighted in yellow on adjacent surface plots). ROIs entered into statistical analyses are illustrated as green shaded area on surface plots. Panel E: Histogram of surprisal values for sentence (green) and word-list (purple) words.

Entropy

Entropy significantly predicted the MEG signal in both sentences and word-lists, however to a lesser extent than the aforementioned predictors. In sentences (see Fig 5 panel A), entropy predicted variance in bilateral occipital, left inferior temporal and frontal parcels, and in the posterior MTG, from 0-242ms, 292-367ms, and at individual time points of 433ms and 525ms (relative to word onset). In word-lists (see Fig 5 panel B), entropy significantly predicted variance in bilateral occipital and inferior temporal cortex from 0-83ms. Significantly more variance was explained by entropy in sentences compared to word-lists in a single left inferior temporal parcel (BA37) 450-458ms after word onset (see Fig 5 panel C).

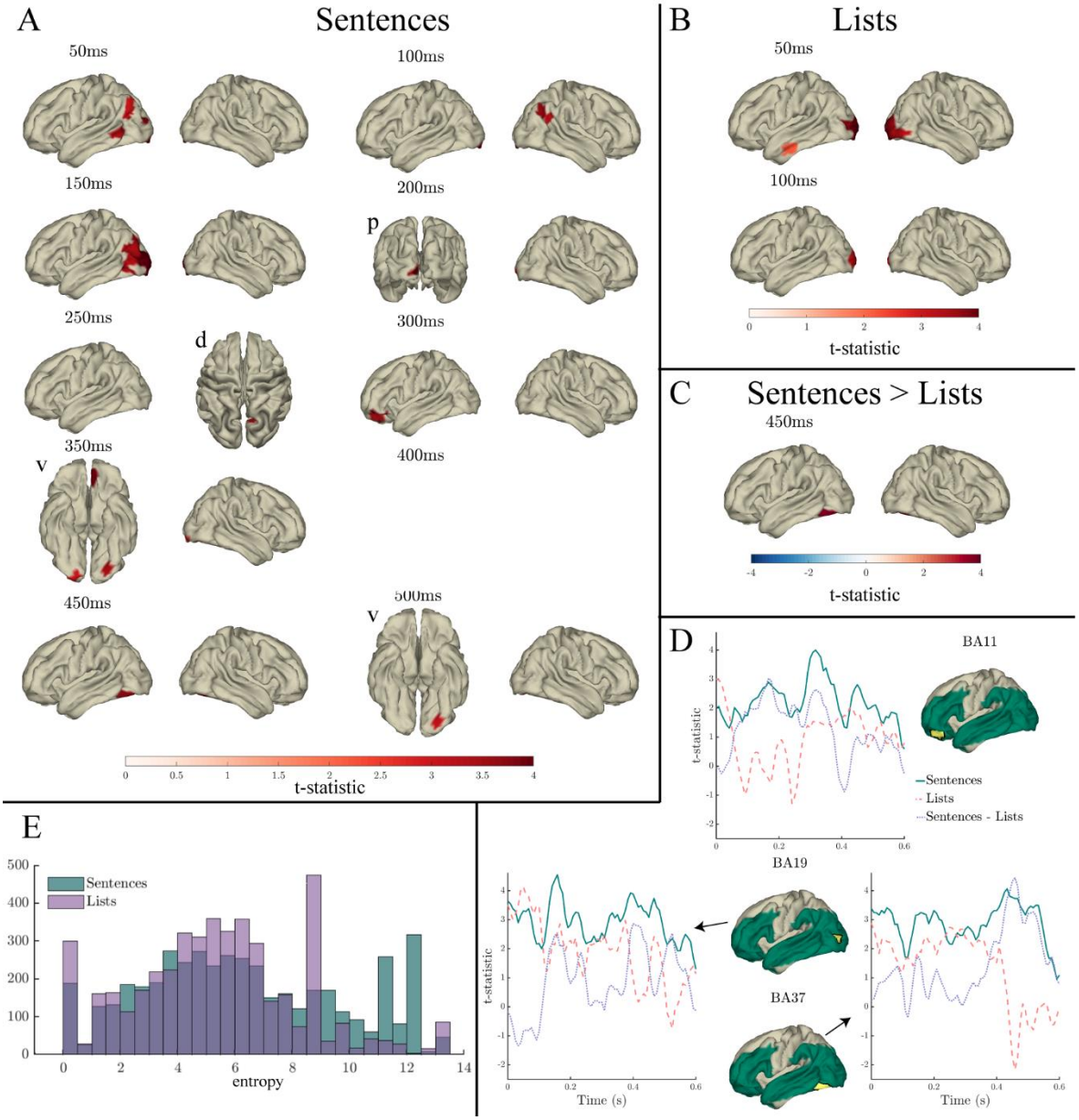

Figure 5. Surface plots of T-statistics (averaged over 50ms time windows centred at the indicated latencies, for visualisation) quantifying the difference in variance explained by entropy, beyond that explained by lexical frequency (log10 transformed), index, surprisal and length, in sentence compared to random permutation models (panel A; $p<.05$ one-sided, corrected), word-list compared to random permutation models (panel B; $p<.05$ one-sided, corrected), and sentence compared to word-list models (panel C; $p<.05$ two-sided, corrected). Parcels for which no time point was significant during the 50ms time bin are masked. Ventral, dorsal, and posterior views are indicated with adjacent "v", "d" and "p" labels, respectively. Panel D: Time courses of T-statistics for sentence (solid green line) and word-list (dashed red line) models compared to random permutation models, and sentence compared to word-list models (dotted purple line) for subparcels of BA11, BA19 and BA37 (highlighted in yellow on adjacent surface plots). ROIs entered into statistical analyses are illustrated as green shaded area on surface plots. Panel E: Histogram of entropy values for sentence (green) and word-list (purple) words.

Condition specific interaction between lexical frequency and index

The above findings show how our model comparison approach identified brain activity patterns that were aligned with word-by-word fluctuations of various quantities that relate to lexical predictability. Considering that the interaction between lexical frequency and context (often quantified with word position in the sentence) has been consistently reported in previous electrophysiological studies (Alday et al., 2017; Dambacher et al., 2006; Payne et al., 2015; Sereno et al., 2019; Van Petten & Kutas, 1990), we conducted an exploratory analysis of this interaction in our data – in parcels that showed conditional differences in effects of either lexical frequency or index (see Figs 2-3) – specifically focussing on the spatial and temporal dynamics of this effect. As effects of the interaction did not survive the stringent multiple comparisons correction (p>.05 corrected), Fig 6 presents the spatiotemporal distributions, along with example time courses, of T-statistics for parcels and time points that were significant without correcting for multiple comparisons (uncorrected p<.05).

Beyond the variance explained by the main effects of index and lexical frequency, the index × lexical frequency interaction explained additional variance in sentences from 150ms after word onset in frontal parcels (BA10/BA11/BA44/BA47), spreading to MTG and posterior STG (BA22/BA38) from 342ms onwards, where effects peaked at around 400ms (see Fig 6 panel A; uncorrected p<.05).

In word-lists, the index × lexical frequency interaction explained additional variance in several time windows throughout the 0-600ms analysis window, predominantly from 300ms onwards, but also at earlier time points. The effect spread from frontal (BA10/BA11) to temporal (BA22/BA38) and inferior frontal (BA44/BA46) parcels, peaking at around 450ms in frontal parcels (see Fig 6 panel B; uncorrected p<.05).

On inspection of Fig 6 panel C, the comparison of the coefficient of determination for the interaction in sentence and word-list models revealed an interesting spatiotemporal pattern of results. During an earlier time window (100-300ms), more variance was explained by the index × lexical frequency interaction in sentences compared to word-lists in frontal parcels (BA10/BA11; warm colours Fig 6 panel C), yet more variance was explained by the index × lexical frequency interaction in word-lists compared to sentences in temporal parcels (BA21/BA22/BA38; cool colours Fig 6 panel C). However, in a later time window (350-500ms) a reverse pattern was observed, where more variance was explained by the interaction in word-lists compared to sentences in frontal parcels, and more variance was explained in sentences compared to word-lists in temporal parcels. This pattern is also evident in the time courses of T-statistics presented in Fig 6 panel D.

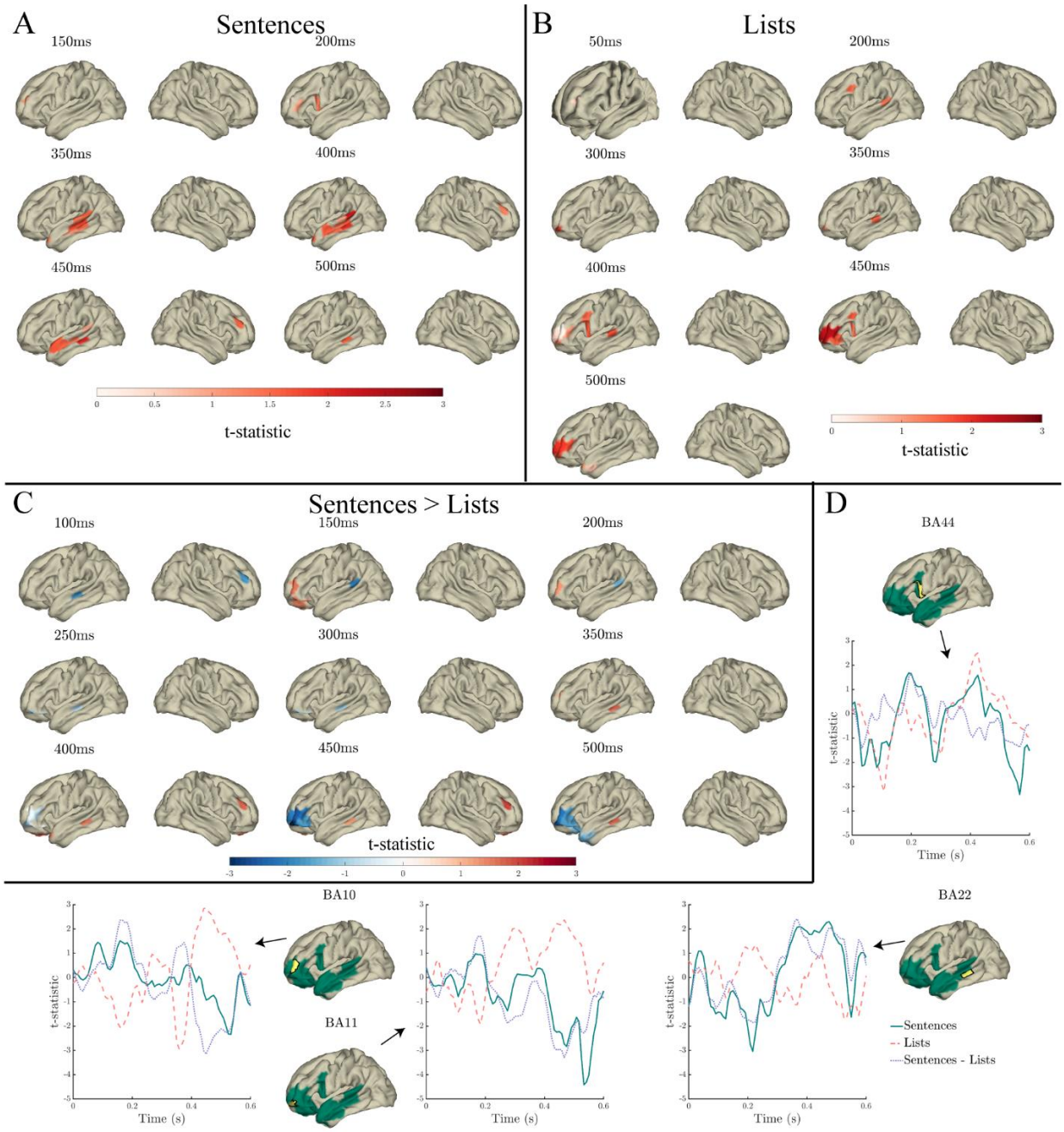

Figure 6. Surface plots of T-statistics (averaged over 50ms time windows centred at the indicated latencies, for visualisation) quantifying the difference in variance explained by lexical frequency × index interaction, beyond that explained by lexical frequency (log10 transformed) and index, in sentence compared to random permutation models (panel A; $p<.05$ one-sided, uncorrected), word-list compared to random permutation models (panel B; $p<.05$ one-sided, uncorrected), and sentence compared to word-list models (panel C; $p<.05$ two-sided, corrected). Parcels for which no time point was significant during the 50ms time bin are masked. Panel D: Time courses of T-statistics for sentence (solid green line) and word-list (dashed red line) models compared to random permutation models, and sentence compared to word-list models (dotted purple line) for subparcels of BA44, BA22, BA10 and BA11 (highlighted in yellow on adjacent surface plots). ROIs entered into statistical analyses are illustrated as green shaded areas on surface plots.

4. Discussion

During sentence reading, the brain processes individual words at a remarkable speed. Such fast processing is not only facilitated and affected by the word's frequency of occurrence within a given language (Calvo & Meseguer, 2002; Inhoff & Rayner, 1986; Rayner & Duffy, 1986; Rubenstein et al., 1970), but also by the word's context, brought about by semantic and syntactic constraints imposed by preceding words (Calvo & Meseguer, 2002; Staub et al., 2015; Van Petten & Kutas, 1990). There is a well-documented discrepancy between the electrophysiological and eye-tracking literature as to whether frequency and context have additive or interactive effects on processing (Kretzschmar et al., 2015). It is unclear whether word frequency influences processing when the input is predictable. The current work aimed to better define the spatiotemporal dynamics of the effects of lexical frequency and predictability on word processing, establish to what extent lexical frequency and predictability independently influence word processing, and to what extent they interact. To this end, we performed state-of-the-art analysis of a large and well-balanced MEG dataset, combining spatiotemporal hyperalignment with cross-validated encoding model comparisons. This allowed us to go beyond the more traditional approaches that use event-related averaging or generalized linear models, thus being able to infer effects based on the brain's response to individual words.

We found that the MEG signal reflects the lexical frequency of individual words throughout the analysis time window beyond effects of predictability, in a network expanding from occipital cortex throughout the left temporal and inferior frontal regions of the language network. Index, surprisal, and entropy additionally each significantly predicted the MEG signal. All comparisons were made while controlling for each alternative predictor, and word length. There were significant but focal differences between sentences and word-lists in the effects of lexical frequency, surprisal and entropy. In contrast to these focal differences, the effect of index differed extensively in sentences compared to word-lists. Thus, out of the analysed predictors, only the effect of index was greatly influenced by the sentential context in which words were presented (i.e. sentences/word-lists). These findings highlight that the word processing mechanisms reflected by index are dependent on the preceding context, whereas the processing mechanisms underlying lexical frequency and surprisal remain largely the same regardless of the degree of sentential context. Finally, although the index × lexical frequency interaction effect was not significant under a conservative multiple comparison correction scheme, an exploration of the uncorrected results uncovered an interesting pattern. Namely, both left temporal and frontal cortical activity seemed to be influenced by the interaction, yet the latency at which this occurred was flipped across conditions. While, in sentences, the interaction was expressed more strongly at early time points in frontal areas and only later in temporal areas, this pattern was reversed for word-lists. In the following paragraphs we discuss the results in more detail.

4.1. Lexical frequency

Overall, lexical frequency was encoded in the MEG signal to a similar extent in sentences and word-lists. This effect was widespread, both in space and time, and thus suggests that lexical frequency generically affects the brain response, likely reflecting less effortful processing of high compared to low frequency words.

Comparing sentences with word-lists, frequency was encoded in the MEG signal earlier in sentences than word-lists in the STG and MTG. Given the association of the MTG with lexical–semantic processing (Friederici, 2012; Hagoort, 2017) and the location of the primary auditory cortex and auditory association areas on the STG, the current results suggest that lexical frequency facilitates aspects of semantic and phonological processing earlier when the word is presented in a sentence than when presented in a word-list. Moreover, significantly more variance was explained in sentences compared to word-lists at 267ms in a single dorsolateral PFC parcel (BA46), an area thought to be involved in executive control during language processing (Hagoort, 2003, 2013, 2017).

4.2. Sentential context and predictability

In line with previous literature (Armeni, Willems, van den Bosch, & Schoffelen, 2019; Hultén, Schoffelen, Uddén, Lam, & Hagoort, 2019; Schuster, Hawelka, Himmelstoss, Richlan, & Hutzler, 2020), the word-by-word association between the MEG signals and the increasingly constrained context (i.e. index), and metrics quantifying (the results of) prediction, presented itself with different spatiotemporal dynamics. These will be discussed in the following paragraphs.

Index

Index explained a significant portion of variance in the MEG signal during the entire critical window in both sentences and word-lists. Moreover, index predicted the MEG signal significantly more in sentences than word-lists, predominantly in anterior temporal and frontal cortex. This latter finding illustrates that it is the progressing sentential context that affects word processing in these regions, rather than more domain-general properties that correlate with index, such as working memory demands. The anterior temporal lobe has been associated with conceptual representations (Peelen & Caramazza, 2012; Rice, Lambon Ralph, & Hoffman, 2015) and syntactic structure building (Brennan et al., 2012), the latter of which is engaged more when words are presented in sentences compared to word-lists. The greater influence of index in sentences compared to word-lists in the inferior frontal gyrus is consistent with the notion of unification, the integration of lexical items within the wider semantic and syntactic context as the sentence unfolds (Hagoort, 2005, 2013).

In line with earlier work (Schuster et al., 2020), index was encoded in the MTG and angular gyrus in sentences. No such effect was observed in these regions for word-lists, although the latter qualitative difference was not significant when directly contrasting conditions. Given the association between MTG activity and lexical-semantic processing (Friederici, 2012; Hagoort, 2017), the effect in MTG could reflect the build-up of richer semantic representations as sentences progress, more so than during the progression of word-lists. The absence of an effect of index in word-lists in the angular gyrus may be consistent with the view that this region is a hub to integrate different types of information extracted by various parts of the language network (Binder & Desai, 2011; Hagoort, 2003, 2019). In contrast to unfolding well-formed sentences, word-lists lack syntactic structure, and therefore do not permit for a meaningful integration of structural cues with, for instance, lexico-semantic information.

Surprisal

We estimated surprisal and entropy using corpus-based statistics, using a tri-gram model on the individual sentences and word-lists. Consistent with our expectations, surprisal was overall larger in word-list words (see Fig. 4 panel E). Yet, aside from subtle differences between sentences and word-lists, as discussed below, the overall spatiotemporal characteristics of MEG signal variance explained by surprisal, on top of the other predictors, was similar between conditions. One tentative explanation for this could be that the inclusion of the index predictor in the 'baseline model' already accounted for a large part of signal variance (albeit to different degrees across conditions), causing the additional information provided by surprisal values to be less distinctive across conditions. The word-by-word fluctuations in surprisal explained widespread, predominantly left-lateralized, brain signals, irrespective of condition. This suggests a relation between our operationalisation of surprisal on the one hand, and more automatic ease-of-integration related processes on the other hand. Although care was taken to scramble sentences in a way so as no more than two consecutive words could be syntactically combined, there is evidence that combinatorial processes are robust to local word swaps (Mollica et al., 2020). In the current data, surprisal seems to reflect the same underlying combinatorial processes in word-lists as in sentences, reflecting the ease-of-integration.

A direct statistical comparison across conditions showed some very focal and short-lived differences. Apart from a very early time window, at around 50ms in the MTG, there was a difference around 400-450ms in orbitofrontal and MTG parcels. Lexical access of written words is thought to occur between 130-150ms (Sereno & Rayner, 2003). It is often difficult to determine whether observed effects of surprisal result from participants predicting the upcoming linguistic input, or from more probable words being easier to integrate (Pickering & Gambi, 2018; Willems, Frank, Nijhof, Hagoort, & van den Bosch, 2016). In the present results, surprisal was encoded in the MEG signal in temporal cortex prior to 130ms (in the sentence condition only), which has previously been argued to imply that some linguistic information about a word

has been pre-activated – here constrained by the previous two words – given that bottom-up lexical retrieval could not yet have taken place (Pickering & Gambi, 2018). In contrast, the later effects of surprisal at 400-450ms in orbitofrontal and MTG parcels could result from either integrative or predictive processes. The orbitofrontal cortex has previously been sensitive to predictability, both of linguistic information (Hofmann et al., 2014) and more generally (Nobre, Coull, Frith, & Mesulam, 1999).

Entropy

Entropy quantifies the uncertainty of the upcoming linguistic content (Pickering & Gambi, 2018; Willems et al., 2016). Entropy significantly predicted the MEG signal in both sentences and word-lists. Notably, the spatial and temporal extent of significant effects were much smaller than those of the other predictors. Here, entropy was encoded in early occipital cortical activity, both in sentences and word-lists. Additionally, in sentences, entropy effects were observed in left frontal cortex around 300ms, and in inferior temporal cortex around 450ms. Effects of prediction in occipital parcels during early time points have previously been used as evidence to support the notion that an active prediction of word form is employed by the brain (Dikker, Rabagliati, Farmer, & Pylkkänen, 2010; Pickering & Gambi, 2018). Given that prediction of upcoming words was not possible in the word-list condition, this account seems unlikely here. An alternative explanation is that, under uncertainty of upcoming linguistic input, more weight is placed on bottom-up (as opposed to top-down) signal, and more resources are allocated to visual processing. In contrast to the more generic interpretation of early entropy effects in visual cortical areas, the later sentence-specific effect in inferior temporal cortex could indeed reflect predictive processing of the word form. This region, often referred to as the visual word form area, is likely to receive top-down signals containing linguistic information about a word (Price & Devlin, 2011; Sharoh et al., 2019).

Entropy presented with a markedly different pattern of results compared to the other prediction metrics, in that only several focal groups of parcels during narrow time points survived multiple comparisons correction. It is evident from the time courses in Fig 5 that the encoding of the MEG signal was temporally less consistent for the entropy models compared to the models presented in Figs 2-4. Similarly, Schuster et al. (2020) found no effect of predictability (entropy) in the haemodynamic response when conducting a whole-brain analysis, and effects were found only in an ROI analysis.

4.3. Lexical frequency × Index interaction

In line with previous work (Alday et al., 2017; Dambacher et al., 2006; Payne et al., 2015; Sereno et al., 2019; Van Petten & Kutas, 1990), we investigated the interaction between lexical frequency and index, both within and across individual conditions. Using a strict multiple comparison correction scheme, we did not find any evidence for this. This suggests that our findings concur with the eye-tracking literature, which

has found an additive effect of lexical frequency and predictability on fixation durations (Kennedy et al., 2013; Kretzschmar et al., 2015; Staub, 2015; Staub & Benatar, 2013). Yet, an exploratory analysis of the nominally thresholded data revealed some interesting condition-specific dynamics.

In left temporal parcels (BA21/BA22/BA38), including the MTG, the interaction explained more variance in word-lists than sentences at early time points, and in sentences compared to word-lists in a later time window. The later (350-500ms) temporal cortex effect is consistent with previous electrophysiological literature that has averaged over central-parietal sensors in an N400 time window, as the interaction explained more variance in sentences than word-lists. Specifically, earlier work has shown that the effect of frequency on the N400 diminishes with increased word position, in sentences but not word-lists (Payne et al., 2015), eliciting the conclusion that lexical frequency no longer influences word processing when there is increased context.

In frontal parcels (BA10/BA11), more variance was explained by the interaction in sentences than word-lists in an early time window, and in word-lists than sentences in a later time window. An interaction between frequency and predictability has similarly been found in orbitofrontal cortex by Hofmann et al. (2014), who found stronger brain responses to disconfirmed predictions for only low and not high frequency words. BA10 has previously been associated with encoding semantic relationships (Bunge et al., 2009; Frankland & Greene, 2020; Knowlton et al., 2012; Ramnani & Owen, 2004). Overall, the difference between sentences and word-lists in the interaction between word frequency and index seems to occur in the time that these factors interact, rather than in the presence of an interaction.

4.4. Limitations and future work

A limitation of the current work is that words were presented word-by-word, causing the stimulation to be externally paced. Yet, it is well known that in more naturalistic settings the reading pace is determined by the reader, where eye movement and fixation behaviour is in part the result of prediction related processes (Rayner & Well, 1996). Indeed, there is evidence to suggest that predictability facilitates processing before a word is fixated, while the word is within parafoveal view (Balota, Pollatsek, & Rayner, 1985; Staub, 2015; Staub & Goddard, 2019). Predictive processes may be engaged at different latencies or to a different extent in natural reading compared to the current paradigm, due to their interaction with executive control of eye movements. Future work should aim to investigate whether the observed spatiotemporal dynamics of the effects of lexical frequency and predictability on the MEG signal hold during naturalistic reading.

4.5. Conclusions

We provide evidence to support that frequency and contextual constraints have identifiable effects on multiple stages of word-by-word processing, from early visual and lexical retrieval to later integration and

unification processes. Largely similar spatiotemporal effects across both sentences and word-lists suggest that lexical frequency generally affects how fast and effortful processing is, independently from ongoing predictive processes.

Although we found no significant effect of a lexical frequency × index interaction with a conservative multiple comparisons correction scheme - consistent with the additive effects of these variables typically observed in the eye-tracking literature - an exploratory (uncorrected) analysis revealed an interesting pattern of results. Namely, the effect of the interaction was reversed in time and space in sentences compared to word-lists. In the MTG, which is associated with lexical-semantic processing, the interaction explained more variance in word-lists than sentences in an early time window, and in sentences than word-lists in a later time window. The latter is consistent with the frequency × index interaction that is typically observed in the N400 time window in sentences but not word-lists (Payne et al., 2015). In orbitofrontal cortex, which has previously been associated with forming semantic relationships, the interaction explained more variance in sentences than word-lists at early time points, but in word-lists than sentences in a later time window. Our findings may contribute to improved models of word reading, which do not yet fully account for effects of predictability (Staub & Goddard, 2019).

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6. References

Alday, P. M., Schlesewsky, M., & Bornkessel-Schlesewsky, I. (2017). Electrophysiology Reveals the Neural Dynamics of Naturalistic Auditory Language Processing: Event-Related Potentials Reflect Continuous Model Updates. *eNeuro, 4*(6). doi:10.1523/ENEURO.0311-16.2017

Arana, S., Marquand, A., Hultén, A., Hagoort, P., & Schoffelen, J.-M. (2020). Sensory Modality-Independent Activation of the Brain Network for Language. *The Journal of Neuroscience, 40*(14), 2914-2924. doi:10.1523/jneurosci.2271-19.2020

Armeni, K., Willems, R. M., van den Bosch, A., & Schoffelen, J.-M. (2019). Frequency-specific brain dynamics related to prediction during language comprehension. *Neuroimage, 198*, 283-295. doi:https://doi.org/10.1016/j.neuroimage.2019.04.083

Balota, D. A., Pollatsek, A., & Rayner, K. (1985). The interaction of contextual constraints and parafoveal visual information in reading. *Cognitive Psychology, 17*(3), 364-390. doi:https://doi.org/10.1016/0010-0285(85)90013-1

Binder, J. R., & Desai, R. H. (2011). The neurobiology of semantic memory. *Trends in Cognitive Sciences, 15*(11), 527-536. doi:https://doi.org/10.1016/j.tics.2011.10.001

Brennan, J., Nir, Y., Hasson, U., Malach, R., Heeger, D. J., & Pylkkänen, L. (2012). Syntactic structure building in the anterior temporal lobe during natural story listening. *Brain and Language, 120*(2), 163-173. doi:https://doi.org/10.1016/j.bandl.2010.04.002

Brysbaert, M. (2019). How many words do we read per minute? A review and meta-analysis of reading rate. *Journal of Memory and Language, 109*. doi:https://doi.org/10.1016h/j.jml.2019.104047

Bunge, S. A., Helskog, E. H., & Wendelken, C. (2009). Left, but not right, rostrolateral prefrontal cortex meets a stringent test of the relational integration hypothesis. *Neuroimage, 46*(1), 338-342. doi:https://doi.org/10.1016/j.neuroimage.2009.01.064

Calvo, M. G., & Meseguer, E. (2002). Eye Movements and Processing Stages in Reading: Relative Contribution of Visual, Lexical, and Contextual Factors. *The Spanish Journal of Psychology, 5*(1), 66-77. doi:10.1017/S1138741600005849

Catani, M., Allin, M. P. G., Husain, M., Pugliese, L., Mesulam, M. M., Murray, R. M., & Jones, D. K. (2007). Symmetries in human brain language pathways correlate with verbal recall. *Proceedings of the National Academy of Sciences, 104*(43), 17163-17168. doi:10.1073/pnas.0702116104

Chee, M. W. L., Hon, N. H. H., Caplan, D., Lee, H. L., & Goh, J. (2002). Frequency of Concrete Words Modulates Prefrontal Activation during Semantic Judgments. *Neuroimage, 16*(1), 259-268. doi:https://doi.org/10.1006/nimg.2002.1061

Dambacher, M., Dimigen, O., Braun, M., Wille, K., Jacobs, A. M., & Kliegl, R. (2012). Stimulus onset asynchrony and the timeline of word recognition: Event-related potentials during sentence reading. *Neuropsychologia, 50*(8), 1852-1870. doi:https://doi.org/10.1016/j.neuropsychologia.2012.04.011

Dambacher, M., Kliegl, R., Hofmann, M., & Jacobs, A. M. (2006). Frequency and predictability effects on event-related potentials during reading. *Brain Research, 1084*(1), 89-103. doi:https://doi.org/10.1016/j.brainres.2006.02.010

Dikker, S., Rabagliati, H., Farmer, T. A., & Pylkkänen, L. (2010). Early Occipital Sensitivity to Syntactic Category Is Based on Form Typicality. *Psychological Science, 21*(5), 629-634. doi:10.1177/0956797610367751

Engbert, R., Nuthmann, A., Richter, E. M., & Kliegl, R. (2005). SWIFT: A Dynamical Model of Saccade Generation During Reading. *Psychological Review, 112*(4), 777-813. doi:10.1037/0033-295X.112.4.777

Frankland, S. M., & Greene, J. D. (2020). Two Ways to Build a Thought: Distinct Forms of Compositional Semantic Representation across Brain Regions. *Cerebral Cortex, 30*(6), 3838-3855. doi:10.1093/cercor/bhaa001

Friederici, A. D. (2009). Pathways to language: fiber tracts in the human brain. *Trends in Cognitive Sciences, 13*(4), 175-181. doi:https://doi.org/10.1016/j.tics.2009.01.001

Friederici, A. D. (2012). The cortical language circuit: from auditory perception to sentence comprehension. *Trends in Cognitive Sciences, 16*(5), 262-268. doi:https://doi.org/10.1016/j.tics.2012.04.001

Glasser, M. F., & Rilling, J. K. (2008). DTI Tractography of the Human Brain's Language Pathways. *Cerebral Cortex, 18*(11), 2471-2482. doi:10.1093/cercor/bhn011

Hagoort, P. (2003). How the brain solves the binding problem for language: a neurocomputational model of syntactic processing. *Neuroimage, 20*, S18-S29. doi:https://doi.org/10.1016/j.neuroimage.2003.09.013

Hagoort, P. (2005). On Broca, brain, and binding: a new framework. *Trends in Cognitive Sciences, 9*(9), 416-423. doi:https://doi.org/10.1016/j.tics.2005.07.004

Hagoort, P. (2013). MUC (Memory, Unification, Control) and beyond. *Frontiers in Psychology, 4*(416). doi:10.3389/fpsyg.2013.00416

Hagoort, P. (2017). The core and beyond in the language-ready brain. *Neuroscience & Biobehavioral Reviews*.

Hagoort, P. (2019). The meaning-making mechanism(s) behind the eyes and between the ears. *Philosophical Transactions of the Royal Society B: Biological Sciences, 375*(1791). doi:doi:10.1098/rstb.2019.0301

Hagoort, P., Baggio, G., & Willems, R. M. (2009). Semantic unification. In *The cognitive neurosciences, 4th ed.* (pp. 819-836): MIT press.

Hofmann, M. J., Dambacher, M., Jacobs, A. M., Kliegl, R., Radach, R., Kuchinke, L., . . . Herrmann, M. J. (2014). Occipital and orbitofrontal hemodynamics during naturally paced reading: An fNIRS study. *Neuroimage, 94*, 193-202. doi:https://doi.org/10.1016/j.neuroimage.2014.03.014

Huettig, F. (2015). Four central questions about prediction in language processing. *Brain Research, 1626*, 118-135. doi:https://doi.org/10.1016/j.brainres.2015.02.014

Hultén, A., Schoffelen, J.-M., Uddén, J., Lam, N. H. L., & Hagoort, P. (2019). How the brain makes sense beyond the processing of single words – An MEG study. *Neuroimage, 186*, 586-594. doi:https://doi.org/10.1016/j.neuroimage.2018.11.035

Inhoff, A. W., & Rayner, K. (1986). Parafoveal word processing during eye fixations in reading: Effects of word frequency. *Perception & Psychophysics, 40*(6), 431-439.

Kennedy, A., Pynte, J., Murray, W. S., & Paul, S.-A. (2013). Frequency and predictability effects in the Dundee Corpus: An eye movement analysis. *The Quarterly Journal of Experimental Psychology, 66*(3), 601-618. doi:10.1080/17470218.2012.676054

Knowlton, B. J., Morrison, R. G., Hummel, J. E., & Holyoak, K. J. (2012). A neurocomputational system for relational reasoning. *Trends in Cognitive Sciences, 16*(7), 373-381. doi:https://doi.org/10.1016/j.tics.2012.06.002

Kretzschmar, F., Schlesewsky, M., & Staub, A. (2015). Dissociating Word Frequency and Predictability Effects in Reading: Evidence From Coregistration of Eye Movements and EEG. *Journal of Experimental Psychology-Learning Memory and Cognition, 41*(6), 1648-1662. doi:10.1037/xlm0000128

Kutas, M., & Federmeier, K. D. (2011). Thirty Years and Counting: Finding Meaning in the N400 Component of the Event-Related Brain Potential (ERP). *Annual Review of Psychology, 62*(1), 621-647. doi:10.1146/annurev.psych.093008.131123

Mollica, F., Siegelman, M., Diachek, E., Piantadosi, S. T., Mineroff, Z., Futrell, R., . . . Fedorenko, E. (2020). Composition is the Core Driver of the Language-selective Network. *Neurobiology of Language, 1*(1), 104-134. doi:10.1162/nol_a_00005

Nobre, A. C., Coull, J. T., Frith, C. D., & Mesulam, M. M. (1999). Orbitofrontal cortex is activated during breaches of expectation in tasks of visual attention. *Nature Neuroscience, 2*(1), 11-12. doi:10.1038/4513

Nolte, G. (2003). The magnetic lead field theorem in the quasi-static approximation and its use for magnetoencephalography forward calculation in realistic volume conductors. *Physics in Medicine & Biology, 48*(22), 3637.

Payne, B. R., Lee, C. L., & Federmeier, K. D. (2015). Revisiting the incremental effects of context on word processing: Evidence from single-word event-related brain potentials. *Psychophysiology, 52*(11), 1456-1469. doi:10.1111/psyp.12515

Peelen, M. V., & Caramazza, A. (2012). Conceptual Object Representations in Human Anterior Temporal Cortex. *The Journal of Neuroscience, 32*(45), 15728-15736. doi:10.1523/jneurosci.1953-12.2012

Pickering, M. J., & Gambi, C. (2018). Predicting While Comprehending Language: A Theory and Review. *Psychological Bulletin, 144*(10), 1002-1044. doi:10.1037/bul0000158

Price, C. J., & Devlin, J. T. (2011). The Interactive Account of ventral occipitotemporal contributions to reading. *Trends in Cognitive Sciences, 15*(6), 246-253. doi:https://doi.org/10.1016/j.tics.2011.04.001

Ramnani, N., & Owen, A. M. (2004). Anterior prefrontal cortex: insights into function from anatomy and neuroimaging. *Nature Reviews Neuroscience, 5*(3), 184-194. doi:10.1038/nrn1343

Rayner, K. (1986). Eye movements and the perceptual span in beginning and skilled readers. *Journal of Experimental Child Psychology, 41*(2), 211-236. doi:10.1016/0022-0965(86)90037-8

Rayner, K., & Duffy, S. A. (1986). Lexical complexity and fixation times in reading: Effects of word frequency, verb complexity, and lexical ambiguity. *Memory & Cognition, 14*(3), 191-201.

Rayner, K., & Well, A. D. (1996). Effects of contextual constraint on eye movements in reading: A further examination. *Psychonomic Bulletin & Review, 3*(4), 504-509.

Reichle, E. D., Rayner, K., & Pollatsek, A. (2003). The E-Z Reader model of eye-movement control in reading: Comparisons to other models. *Behavioral and Brain Sciences, 26*(4), 445-476. doi:10.1017/S0140525X03000104

Rice, G. E., Lambon Ralph, M. A., & Hoffman, P. (2015). The Roles of Left Versus Right Anterior Temporal Lobes in Conceptual Knowledge: An ALE Meta-analysis of 97 Functional Neuroimaging Studies. *Cerebral Cortex, 25*(11), 4374-4391. doi:10.1093/cercor/bhv024

Rubenstein, H., Garfield, L., & Millikan, J. A. (1970). Homographic entries in the internal lexicon. *Journal of Verbal Learning and Verbal Behavior, 9*(5), 487-494. doi:https://doi.org/10.1016/S0022-5371(70)80091-3

Schäfer, R., & Bildhauer, F. (2012). *Building large corpora from the web using a new efficient tool chain.* Paper presented at the LREC.

Schoffelen, J.-M., Hultén, A., Lam, N., Marquand, A. F., Uddén, J., & Hagoort, P. (2017). Frequency-specific directed interactions in the human brain network for language. *Proceedings of the National Academy of Sciences, 114*(30), 8083-8088. doi:10.1073/pnas.1703155114

Schoffelen, J.-M., Oostenveld, R., Lam, N. H. L., Uddén, J., Hultén, A., & Hagoort, P. (2019). A 204-subject multimodal neuroimaging dataset to study language processing. *Scientific Data, 6*(1), 17. doi:10.1038/s41597-019-0020-y

Schuster, S., Hawelka, S., Himmelstoss, N. A., Richlan, F., & Hutzler, F. (2020). The neural correlates of word position and lexical predictability during sentence reading: evidence from fixation-related fMRI. *Language, Cognition and Neuroscience, 35*(5), 613-624. doi:10.1080/23273798.2019.1575970

Sereno, S. C., Brewer, C. C., & O'Donnell, P. J. (2003). Context Effects in Word Recognition:Evidence for Early Interactive Processing. *Psychological Science, 14*(4), 328-333. doi:10.1111/1467-9280.14471

Sereno, S. C., Hand, C. J., Shahid, A., Mackenzie, I. G., & Leuthold, H. (2019). Early EEG correlates of word frequency and contextual predictability in reading. *Language Cognition and Neuroscience*. doi:10.1080/23273798.2019.1580753

Sereno, S. C., & Rayner, K. (2003). Measuring word recognition in reading: eye movements and event-related potentials. *Trends in Cognitive Sciences, 7*(11), 489-493. doi:https://doi.org/10.1016/j.tics.2003.09.010

Sharoh, D., van Mourik, T., Bains, L. J., Segaert, K., Weber, K., Hagoort, P., & Norris, D. G. (2019). Laminar specific fMRI reveals directed interactions in distributed networks during language processing. *Proceedings of the National Academy of Sciences, 116*(42), 21185-21190. doi:10.1073/pnas.1907858116

Smith, M. E., & Halgren, E. (1987). Event-related potentials during lexical decision: effects of repetition, word frequency, pronounceability, and concreteness. *Electroencephalogr Clin Neurophysiol Suppl, 40*, 417-421.

Staub, A. (2015). The Effect of Lexical Predictability on Eye Movements in Reading: Critical Review and Theoretical Interpretation. *Language and Linguistics Compass, 9*(8), 311-327. doi:10.1111/lnc3.12151

Staub, A., & Benatar, A. (2013). Individual differences in fixation duration distributions in reading. *Psychonomic Bulletin & Review, 20*(6), 1304-1311. doi:10.3758/s13423-013-0444-x

Staub, A., & Goddard, K. (2019). The Role of Preview Validity in Predictability and Frequency Effects on Eye Movements in Reading. *Journal of Experimental Psychology-Learning Memory and Cognition, 45*(1), 110-127. doi:10.1037/xlm0000561

Staub, A., Grant, M., Astheimer, L., & Cohen, A. (2015). The influence of cloze probability and item constraint on cloze task response time. *Journal of Memory and Language, 82*, 1-17. doi:10.1016/j.jml.2015.02.004

Van Petten, C., & Kutas, M. (1990). Interactions between sentence context and word frequencyinevent-related brainpotentials. *Memory & Cognition, 18*(4), 380-393. doi:10.3758/bf03197127

Van Veen, B. D., van Drongelen, W., Yuchtman, M., & Suzuki, A. (1997). 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

Willems, R. M., Frank, S. L., Nijhof, A. D., Hagoort, P., & van den Bosch, A. (2016). Prediction During Natural Language Comprehension. *Cerebral Cortex, 26*(6), 2506-2516. doi:10.1093/cercor/bhv075