The Cortical Representation of Language Timescales is Shared between Reading and Listening

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Abstract

Natural language comprehension is thought to involve the integration of low-level sensory representations into a hierarchy of increasingly high-level representations. To investigate whether in the human brain the same pathways are used to integrate both written and spoken language, we tested whether brain representations of this hierarchy are shared between written and spoken language comprehension. Different levels of the language hierarchy were operationally defined as *timescales*, where each timescale refers to the spectral components of a language stimulus that vary over a certain number of words. Voxelwise encoding models were used to determine how different language timescales are represented across the cerebral cortex, for each modality separately. The encoding models were estimated with fMRI BOLD data that were recorded while participants read and listened to the same set of natural language narratives in each modality (Huth et al., 2016; Deniz et al., 2019). These models reveal that the topographic organization of language timescale representations across the cortical surface is highly similar between the two modalities. Our results suggest that brain representations of language timescales are largely independent of stimulus modality.

1 Introduction

Natural language contains a hierarchy of components, ranging from low-level components such as letterforms to high-level components such as narrative arc. Levels of this hierarchy can be operationally defined in terms of the number of words over which they vary. For example, low-level components such as visual letterforms in written language and articulatory features in spoken language vary within the course of single words. Higher-level components vary over increasing numbers of words. In this work we use the term *timescale* to refer to a set of components that vary over a certain number of words.

Theories of human language processing suggest that during language processing, brain representations of low-level sensory timescales are incrementally integrated into representations of higher-level timescales. This integration process is thought to form a topographic organization of representations of different language timescales across the cortical surface (Lerner et al., 2011). Brain representations of low-level timescales that vary within single words are shown to be specific to the modality of stimulus presentation. For example, visual letterforms in written language are represented in the early visual cortex, whereas articulatory features in spoken language are represented in the early auditory cortex (Heilbron et al., 2020; de Heer et al., 2017). On the other hand, many parts of temporal, parietal, and prefrontal cortex process both written and spoken language (e.g., Booth et al., 2002; Buchweitz et al., 2009; Liuzzi et al., 2017; Regev et al., 2013; Deniz et al., 2019; Nakai et al., 2021). However, it is unclear whether within these cortical areas written and spoken language elicit the same or different topographic organizations of language timescale representations. The answer to this question would suggest whether the same pathways are used to integrate written and spoken language.

One way to address this question would be to compare how representations of different timescales are organized across the cortical surface, between written and spoken language comprehension. However, prior work has not provided this comparison. Although prior studies have estimated the topographic organization of timescale representations in the brain during spoken language comprehension

(Lerner et al., 2011; Baldassano et al., 2017; Blank and Fedorenko, 2020; Jain and Huth, 2018; Jain et al., 2020), prior work has not studied the organization of timescale representations during written language comprehension.

In this study, we analyzed functional magnetic resonance imaging (fMRI) recordings from participants who read and listened to the same set of narratives. To transform the stimulus words into features that each reflect a certain timescale of stimulus information, first a language model (BERT) was used to extract contextual embeddings of the narrative stimuli, and then linear filters were used to separate the contextual embeddings into timescale-specific stimulus features. Voxelwise encoding models were used to estimate where different language timescales are represented across the cerebral cortex for reading and listening separately. The organization of these representations was then compared between the two modalities.

2 Results

For each individual participant we compared the organization of language timescale representations between written and spoken language comprehension. Voxel timescale selectivity was compared between reading and listening across the set of voxels that are language-selective for both modalities. The set of language-selective voxels for each modality was identified as those for which timescale-specific language feature spaces significantly predicted blood oxygenation level dependent (BOLD) activity (one-sided permutation test, $p < 0.05$, false discovery rate (FDR) corrected). For each participant, voxel timescale selectivity is significantly positively correlated between the two modalities (S1: $r = 0.41$, S2: $r = 0.58$, S3: $r = 0.44$, S4: 0.34, S5: 0.47, S6: 0.35, S7: 0.40, S8: 0.49, S9: 0.52, $p < 0.001$ for each participant; Figure 1a). Visual inspection of voxel timescale selectivity across the cortical surface confirms that the cortical organization of timescale selectivity is similar between reading and listening (Figure 1b, Figure 1c). For both modalities, timescale selectivity varies along spatial gradients from intermediate timescale selectivity in superior temporal cortex to long timescale selectivity in inferior temporal cortex, and from intermediate timescale selectivity in posterior prefrontal cortex to long timescale selectivity in anterior prefrontal cortex. Medial parietal cortex voxels are selective to long timescales for both modalities. These results suggest that for each individual participant representations of language timescales are organized similarly across the cerebral cortex between reading and listening.

Further analysis of individual participant estimates of timescale selectivity suggest that attentional shifts between novel and known stimuli may cause small differences in timescale selectivity. Activation across higher-level brain regions was more widespread and consistent for the first presentation modality than for the second presentation modality, indicating that participants attend more strongly to novel stimuli (Supplementary Figure 5, Supplementary Figure 6). In six of the nine participants, timescale selectivity was slightly longer for the first presented modality than for the second presented modality (Supplementary Figure 7). This change in timescale selectivity between novel and repeated stimuli suggests that the predictability of high-level narrative components in known stimuli may reduce brain responses to longer language timescales. Nevertheless, the overall cortical organization of timescale selectivity was consistent between reading and listening across all nine participants, regardless of whether they first read or listened to the narratives. This consistency indicates that the effects of stimulus repetition on timescale selectivity are small relative to the similarities between timescale selectivity during reading and listening.

In order to consolidate estimates of timescale selectivity across all participants, we additionally computed group-level estimates of timescale selectivity. To compute group-level estimates, first the estimates for each individual participant were projected to the standard FreeSurfer fsaverage vertex space(Fischl et al., 1999). Then for each vertex the group-level estimate of timescale selectivity was computed as the mean of the fsaverage-projected values. This mean was computed across the set of participants in whom the vertex was language-selective. Group-level estimates were computed separately for reading and listening. Group-level timescale selectivity was then compared between reading and listening across the set of vertices that were significantly predicted in at least one-third of the participants for both modalities. (Supplementary Figure 8 shows the number of participants for which each vertex was significantly predicted in each modality.) This comparison showed that timescale selectivity is highly correlated between reading and listening at the group level ($r = 0.48$; Figure 2a). Cortical maps of group-level timescale selectivity (Figure 2b) visually highlight that the spatial gradients of timescale selectivity across temporal and prefrontal cortices are highly similar

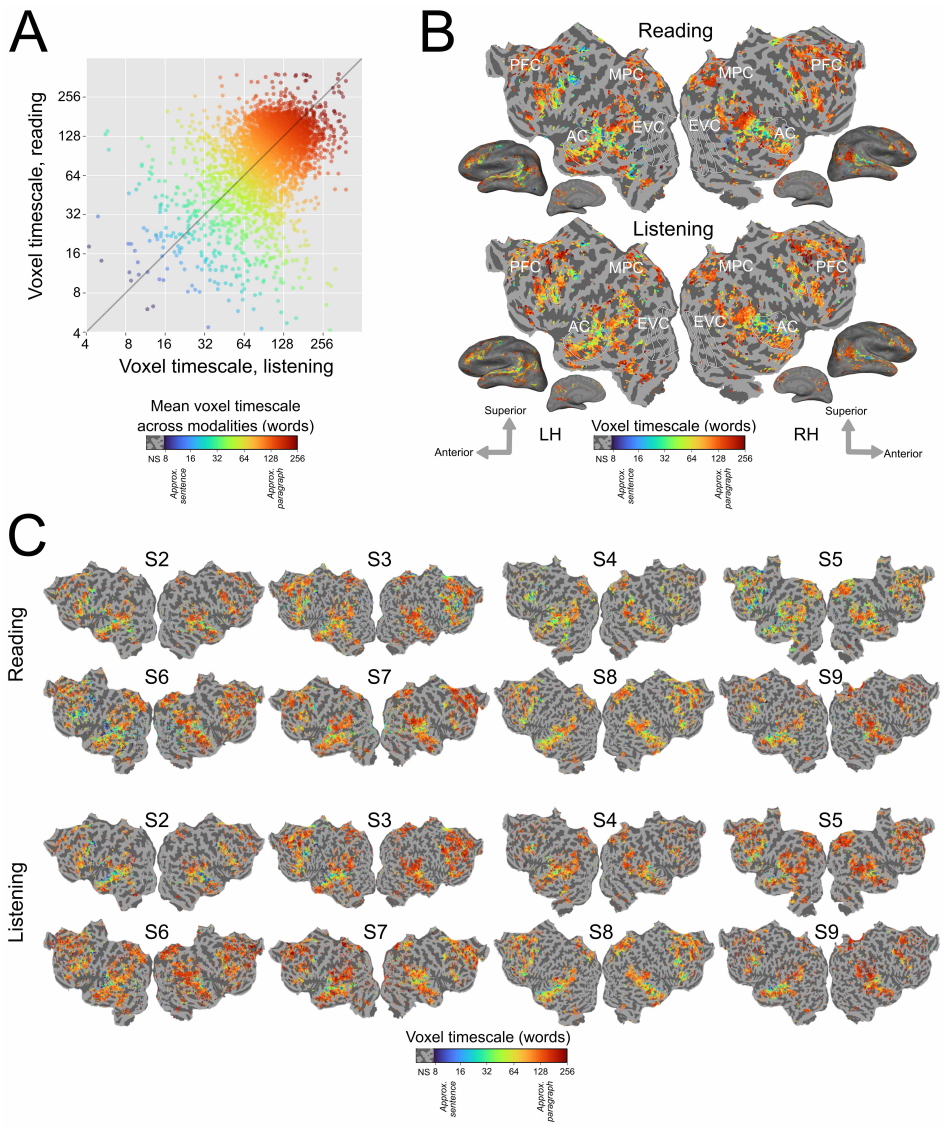

Figure 1: **Timescale selectivity across the cortical surface.** Voxelwise modeling was used to determine the selectivity of each voxel to different language timescales, for reading and listening separately. The timescale selectivity of each voxel was computed as the mean timescale to which the voxel is selective. (See Section 4 for details). A. Timescale selectivity during listening (x-axis) vs reading (y-axis) is shown for one representative participant. Each point represents one voxel that was significantly predicted in both modalities. Each point is colored according to the mean of the timescale selectivity during reading and listening. Blue denotes selectivity to short timescales, green denotes selectivity to intermediate timescales, and red denotes selectivity to long timescales. Timescale selectivity is significantly positively correlated between the two modalities ($r = 0.41$, $p < 0.001$). Timescale selectivity was also significantly positively correlated in the other eight participants (S2: $r = 0.58$, S3: $r = 0.44$, S4: 0.34, S5: 0.47, S6: 0.35, S7: 0.40, S8: 0.49, S9: 0.52, $p < 0.001$ for each participant). B. Timescale selectivity during reading and listening is shown on the flattened cortical surface of the participant shown in Panel A. For each significantly predicted voxel, timescale selectivity is shown according to the color scale at the bottom (same color scale as in Panel A). Voxels that were not significantly predicted are shown in grey. (One-sided permutation test, $\alpha = 0.05$, FDR corrected; LH, left hemisphere; RH, right hemisphere; NS, not significant; PFC=prefrontal cortex, MPC=medial parietal cortex, EVC=early visual cortex, AC=auditory cortex). For both modalities, temporal cortex contains a spatial gradient from intermediate to long timescale selectivity along the superior to inferior axis, prefrontal cortex (PFC) contains a spatial gradient from intermediate to long timescale selectivity along the posterior to anterior axis, and precuneus is predominantly selective to long timescales. C. Voxel timescale selectivity in eight other participants. The format is the same as in Panel B. Note that in most participants, voxels were selective to slightly longer timescales for the first presented modality than for the second presented modality, possibly indicating a small effect of stimulus repetition on timescale selectivity (Supplementary Figure 7). The cortical representation of different language timescales is consistent between reading and listening across temporal, parietal, and prefrontal cortices.

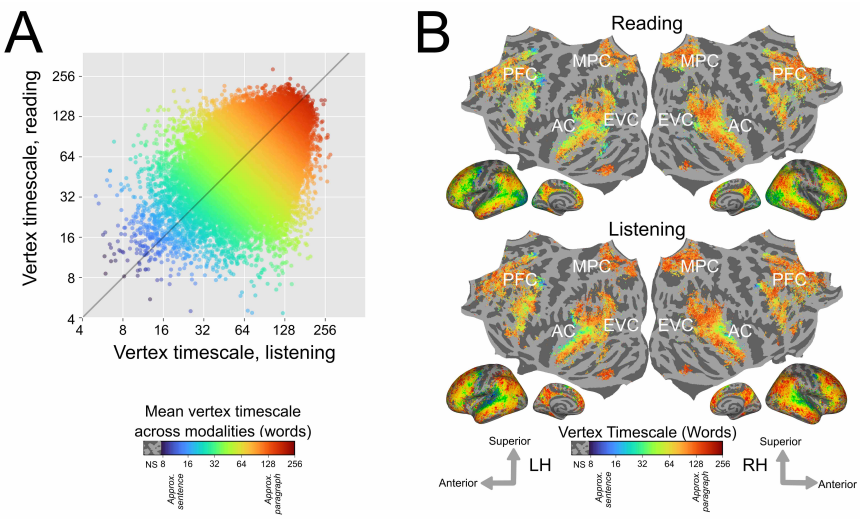

Figure 2: **Group-level estimates of timescale selectivity in standard brain space.** Group-level estimates of timescale selectivity is shown in a standard fsaverage vertex space. The Group-level estimate for each vertex was computed by taking the mean over all participants in whom the vertex was language-selective. A. Group-level timescale selectivity during listening (x-axis) vs reading (y-axis). Each point represents one vertex that was significantly predicted in both modalities for at least one-third of the participants. Each point is colored according to the mean of the group-level timescale selectivity during reading and listening. Blue denotes selectivity to short timescales, green denotes selectivity to intermediate timescales, and red denotes selectivity to long timescales. Timescale selectivity is positively correlated between the two modalities ($r = 0.48$). B. For reading and listening separately the group-level timescale selectivity is shown according to the color scale at the bottom (same color scale as in Panel A). Colored vertices were significantly predicted for both modalities in at least one-third of the participants. Vertices that were not significantly predicted for any participants are shown in grey (one-sided permutation test, $p < 0.05$, FDR corrected; NS, not significant; PFC=prefrontal cortex, MPC=medial parietal cortex, EVC=early visual cortex, AC=auditory cortex). Group-averaged measurements of timescale selectivity are consistent with measurements observed in individual participants (Figure 1, Supplementary Figure 7). For both modalities, there are spatial gradients from intermediate to long timescale selectivity along the superior to inferior axis of temporal cortex, and along the posterior to anterior axis of prefrontal cortex (PFC). Precuneus is predominantly selective to long timescales for both modalities. Across participants, the cortical representation of different language timescales is consistent between reading and listening across temporal, parietal, and prefrontal cortices.

between the two modalities. These group-level results indicate that across participants, representations of language timescales are organized in the same way between reading and listening.

The results shown in Figure 1 and Figure 2 indicate that timescale selectivity is similar between reading and listening. However, one potential confound is that a voxel with the same timescale selectivity for reading and listening could nevertheless have different selectivities to *individual* timescales between the two modalities. To address this possibility, we tested whether selectivity to each of the eight timescales is distributed similarly across the cerebral cortex during reading and listening. For each timescale separately, we computed the correlation between selectivity to that timescale during reading and listening across the set of voxels that are language-selective in both modalities. The correlations for each timescale and participant are shown in Figure 3a. A full table of correlations and statistical significance is shown in Supplementary Table 1. Selectivity to each timescale was positively correlated between reading and listening for each timescale and in each individual participant. Most of these correlations were statistically significant (one-sided permutation test, $\alpha = 0.05$, FDR-corrected). Note that comparing the timescale selectivity metric is more robust to noise in the data than comparing selectivity to each timescale separately. (See Section 4.5 for details.) Therefore correlations between selectivity to each individual timescale are less consistent across participants than correlation between timescale selectivity.

The cortical distribution of selectivity to each timescale is shown for reading and listening separately in Figure 3b. For concision these results are shown at the group-level. Visual inspection of 3b shows that for both reading and listening, short timescales (2-4 words, 4-8 words, 8-16 words)

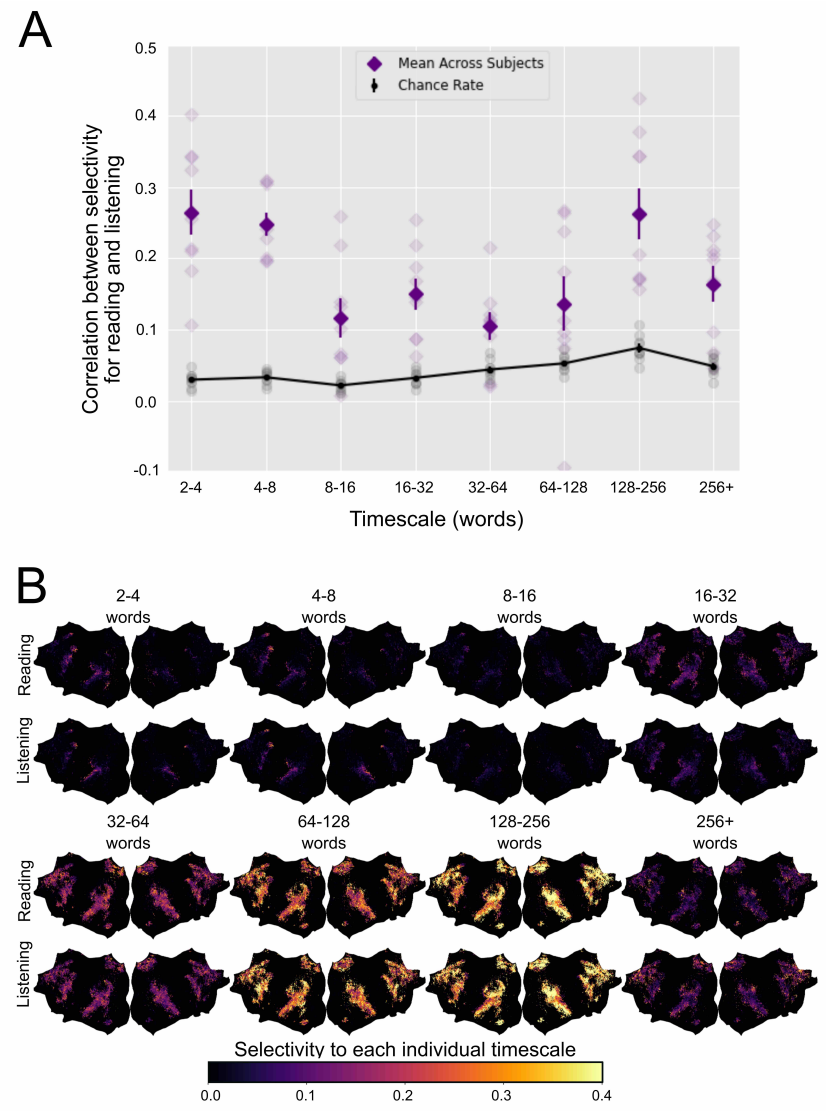

Figure 3: **Similarity of selectivity to each timescale between reading and listening.** To determine whether each individual timescale is represented in similar cortical areas during reading and listening, selectivity to each individual timescale was compared between reading and listening across the cerebral cortex. For each voxel, selectivity to each individual timescale describes the extent to which the corresponding timescale-selective feature space explains variation in BOLD responses, relative to the other timescale-selective feature spaces (see Section 4.5 for details). A. For each timescale the Pearson correlation coefficient was computed between selectivity to that timescale during reading and listening across all voxels that were significantly predicted for both modalities. For each timescale, the mean true correlation across participants is indicated by dark purple diamonds. The mean chance correlation across participants at each timescale is indicated by black dots. (For clarity, these black dots are connected by a black line.) Vertical lines through purple diamonds and black dots are error bars that indicate the standard error of measurement (SEM) across participants for the respective value. True and chance correlations for each individual participant are respectively indicated by light purple diamonds and grey dots. The true correlation is significantly higher than chance in most individual participants and timescales; see Supplementary Table 1 for details. B. The group-level selectivity of each vertex to each timescale is shown in fsaverage space for reading and listening separately. Vertices that were not language-selective in both modalities are shown in black. Outside of primary sensory areas, selectivity to each timescale is distributed similarly across the cortical surface between both modalities. Among voxels that are language-selective in both modalities, each language timescale is represented similarly for reading and listening. These results further indicate that representations of different language timescales are organized in the same way between reading and listening.

are represented in posterior prefrontal cortex and superior temporal cortex; intermediate timescales (16-32 words, 32-64 words) are represented broadly across temporal, prefrontal, and medial parietal cortices; and long timescales (64-128 words, 128-256 words, 256+ words) are represented in prefrontal cortex, precuneus, temporal parietal junction, and inferior temporal cortex. The correlations between selectivity to each timescale and qualitative comparisons of the cortical distribution of selectivity to each timescale between reading and listening indicate that representations of language timescales are organized similarly between reading and listening.

3 Discussion

The purpose of this study was to determine whether a change in stimulus modality would change the organization of representations of language timescales across the cerebral cortex. To address this question, we used voxelwise encoding models to determine the selectivity of each voxel to different language timescales and then compared the organization of these representations between the two modalities (Figure 4). These comparisons show that timescale selectivity is highly correlated between reading and listening across voxels that are language-selective to both modalities in individual participants (Figure 1) and at the group-level (Figure 2). For both modalities, voxel timescale selectivity forms spatial gradients from intermediate to long timescales across prefrontal and temporal cortex, with long timescales in precuneus for both modalities. Moreover, comparisons of selectivity to each timescale separately show that the cortical representation of each timescale is similar between reading and listening (Figure 3). These results suggest that in individual participants there is a topographic organization of language processing timescales that is shared across stimulus modalities.

In this study we introduce a new method for estimating timescale selectivity. This method addresses limitations in methods that have previously been used to determine how different language timescales are processed in the brain during auditory speech comprehension (Lerner et al., 2011; Blank and Fedorenko, 2020; Baldassano et al., 2017; Jain and Huth, 2018; Jain et al., 2020). Some methods require the use of stimuli that are scrambled at different temporal granularities (Lerner et al., 2011; Blank and Fedorenko, 2020). However, artificially scrambled stimuli may cause attentional shifts that evoke brain responses that are not representative of brain responses to natural stimuli (Hamilton and Huth, 2020; Hasson et al., 2010; Deniz et al., 2021). By using voxelwise modeling, we can instead estimate timescale selectivity with brain responses to ecologically valid stimuli. Another study measured the rate of change in patterns of brain activity in order to determine the temporal granularity of representations in each brain region (Baldassano et al., 2017). However, the approach used in Baldassano et al. (2017) did not provide an explicit stimulus-response model that can explain which specific stimulus features can explain the activity in each voxel. Voxelwise modeling allows us to obtain an explicit stimulus-response model that explains which timescale-specific stimulus features evoked responses in each voxel. A separate study that used voxelwise modeling to estimate cortical timescale selectivity exploited the temporal integration mechanism of a specific neural network architecture in order to construct timescale-specific features (Jain et al., 2020; Mahto et al., 2021). However, this mechanism and neural network may not produce the most accurate models of brain responses (see e.g., Toneva and Wehbe (2019); Schrimpf et al. (2020)). Our method instead uses spectral analysis to extract stimulus features that reflect different language timescales, decoupling the feature extraction process from specific neural network architectures. This decoupling enables the construction of encoding models that are more accurate and that are also interpretable in terms of timescale selectivity. In sum, the method for estimating timescale selectivity that we developed in this study allowed us to produce more interpretable, accurate, and ecologically valid models of language timescales in the brain than previous methods.

One limitation of our study comes from the temporal resolution of BOLD data. The data used in this study have a repetition time (TR) of 2 seconds. Therefore, our analysis is unable to detect temporally fine-grained distinctions in timescale selectivity between reading and listening that may occur at the subword level. Future work could apply our method to brain recordings with more fine-grained temporal resolution (e.g., from electrocorticography (ECoG) or electroencephalography (EEG) recordings) to determine whether there are subtle differences in timescale selectivity between modalities. A second limitation arises from the order of stimulus presentation. Each participant first read all eleven stories before listening, or vice versa. Although timescale selectivity was broadly consistent across participants regardless of which modality was presented first, future experiments with

interleaved stimulus presentation modalities might identify small differences in timescale selectivity between the two modalities.

In order to further inform theories of language integration in the brain, our approach of analyzing language timescales could be combined with approaches that analyze brain representations of specific classical language constructs. Approaches based on specific classical language constructs such as part-of-speech tags (Wehbe et al., 2014) and hierarchical syntactic constructs (Hale et al., 2015; Brennan et al., 2016) provide intuitive interpretations of cortical representations, but these language constructs do not encompass all the information that is conveyed in a natural language stimulus. For example, discourse structure and narrative processes are difficult to separate and define. This difficulty is particularly acute for freely produced stimuli, which do not have explicitly marked boundaries between sentences and paragraphs. In contrast, our approach uses spectral analysis to operationally separate language timescales. The resulting models of brain responses can therefore take into account stimulus language information beyond language constructs that can be clearly separated and defined. Evidence from these two approaches could be combined in order to improve our understanding of language processing in the brain. For example, previous studies suggested that hierarchical syntactic structure may be represented in the left temporal lobe, areas in which our analyses identified a spatial gradient from intermediate to long timescale selectivity Brennan et al. (2016). In the future, evidence derived from both approaches should be further compared to inform neurolinguistic theories with a spatially and temporally fine-grained model of voxel representation that can be interpreted in terms of classical language constructs.

In sum, we developed a sensitive, data-driven method to determine whether language timescales are represented in the same way during reading and listening across cortical areas that represent both written and spoken language. Analyses of timescale selectivity in individual participants and at the group level reveal that the cortical representation of different language timescales is highly similar between reading and listening across temporal, parietal, and prefrontal cortices at the level of individual voxels. The shared organization of cortical language timescale selectivity suggests that a change stimulus modality alone does not substantially alter the organization of representations of language timescales. A remaining open question is whether a change in the temporal constraints of language processing would alter the organization of representations of language timescales. One interesting direction for future work would be to compare whether a change in the stimulus presentation method (e.g., static text presentation compared to transient rapid serial visual presentation (RSVP)) would alter the organization of language timescale representations.

4 Methods

Functional MRI was used to record BOLD activity while human participants read and listened to a set of English narrative stories (Huth et al., 2016; Deniz et al., 2019). The stimulus narratives were transformed into feature spaces that each reflect a particular set of language timescales. Each timescale was defined as the spectral components of the stimulus narrative that vary over a certain number of words. These timescale-specific feature spaces were then used to estimate voxelwise encoding models that describe how different timescales of language are represented in the brain for each modality and participant separately. The voxelwise encoding models were used to determine the language timescale selectivity of each voxel, for each participant and modality separately. The language timescale selectivity of individual voxels was compared between reading and listening. The experimental procedure is summarized in Figure 4 and is detailed in the following subsections.

All model fitting and analysis was performed using custom software written in Python, making heavy use of NumPy (Harris et al., 2020), SciPy (Virtanen et al., 2020), Matplotlib (Hunter, 2007), Himalaya (Dupré la Tour et al., 2022), and Pycortex (Gao et al., 2015).

4.1 MRI data collection

MRI data were collected on a 3T Siemens TIM Trio scanner located at the UC Berkeley Brain Imaging Center. A 32-channel Siemens volume coil was used for data acquisition. Functional scans were collected using gradient echo EPI water excitation pulse sequence with the following parameters: repetition time (TR) 2.0045 s; echo time (TE) 31 ms; flip angle 70 degrees; voxel size 2.24 x 2.24 x 4.1 mm (slice thickness 3.5 mm with 18% slice gap); matrix size 100 x 100; and field of view 224 x 224

mm. To cover the entire cortex, 30 axial slices were prescribed and these were scanned in interleaved order. A custom-modified bipolar water excitation radiofrequency (RF) pulse was used to avoid signal from fat. Anatomical data were collected using a T1-weighted multi-echo MP-RAGE sequence on the same 3T scanner.

To minimize head motion during scanning and to optimize alignment across sessions, each participant wore a customized, 3D-printed or milled head case that matched precisely the shape of each participant's head (Gao, 2015; Power et al., 2019). In order to account for inter-session variability, within each session MRI data were z-scored across time for each voxel separately. The data presented here have been presented previously as part of other studies that examined questions unrelated to timescales in language processing (Huth et al., 2016; de Heer et al., 2017; Deniz et al., 2019). Motion correction and automatic alignment were performed on the fMRI data using the FMRIB Linear Image Registration Tool (FLIRT) from FSL 5.0 (Jenkinson et al., 2012). Low-frequency voxel response drift was removed from the data using a third-order Savitzky-Golay filter with a 120s window. (For data preprocessing details see Deniz et al. (2019).)

4.2 Participants

Functional data were collected on nine participants (six males and three females) between the ages of 24 and 36. All procedures were approved by the Committee for Protection of Human Subjects at the University of California, Berkeley. All participants gave informed consent. All participants were healthy, had normal hearing, and had normal or corrected-to-normal vision. The Edinburgh handedness inventory (Oldfield, 1971) indicated that one participant was left handed. The remaining eight participants were right handed or ambidextrous.

Because the current study used a voxelwise encoding model framework, each participant's data were analyzed individually, and both statistical significance and out-of-set prediction accuracy (i.e., generalization) are reported for each participant separately. Because each participant provides a complete replication of all hypothesis tests, sample size calculations were neither required nor performed.

4.3 Stimuli

Human participants read and listened to a set of English narrative stories while in the fMRI scanner. The same stories were used as stimuli for reading and listening sessions and the same stimuli were presented to all participants. These stories were originally presented at The Moth Radio Hour. In each story, a speaker tells an autobiographical story in front of a live audience. The selected stories cover a wide range of topics and are highly engaging. The stories were separated into a model training dataset and a model test dataset. The model training dataset consisted of ten 10-15 min stories. The model test dataset consisted of one 10 min story. This test story was presented twice in each modality (once during each scanning session). The responses to the test story were averaged within each modality. (For details see Huth et al. (2016) and Deniz et al. (2019)). Each story was played during a separate fMRI scan. The length of each scan was tailored to the story and included 10s of silence both before and after the story. Listening and reading presentation order was counterbalanced across participants.

During listening sessions the stories were played over Sensimetrics S14 in-ear piezoelectric headphones. During reading sessions the words of each story were presented one-by-one at the center of the screen using a rapid serial visual presentation (RSVP) procedure (Forster, 1970; Buchweitz et al., 2009). Each word was presented for a duration precisely equal to the duration of that word in the spoken story. The stories were shown on a projection screen at 13 x 14 degrees of visual angle. Participants were asked to fixate while reading the text. (For details see Deniz et al. (2019).)

4.4 Voxelwise encoding models

Voxelwise modeling (VM) was used to model BOLD activity (Wu et al., 2006; Naselaris et al., 2011; Huth et al., 2016; de Heer et al., 2017; Deniz et al., 2019). In the VM framework, stimulus and task parameters are nonlinearly transformed into sets of features (also called "feature spaces") that are hypothesized to be represented in brain activity. Linearized regression is used to estimate a separate model for each voxel. Each model predicts brain activity from each feature space (a model that predicts brain activity from stimulus features is referred to as an "encoding model"). The encoding

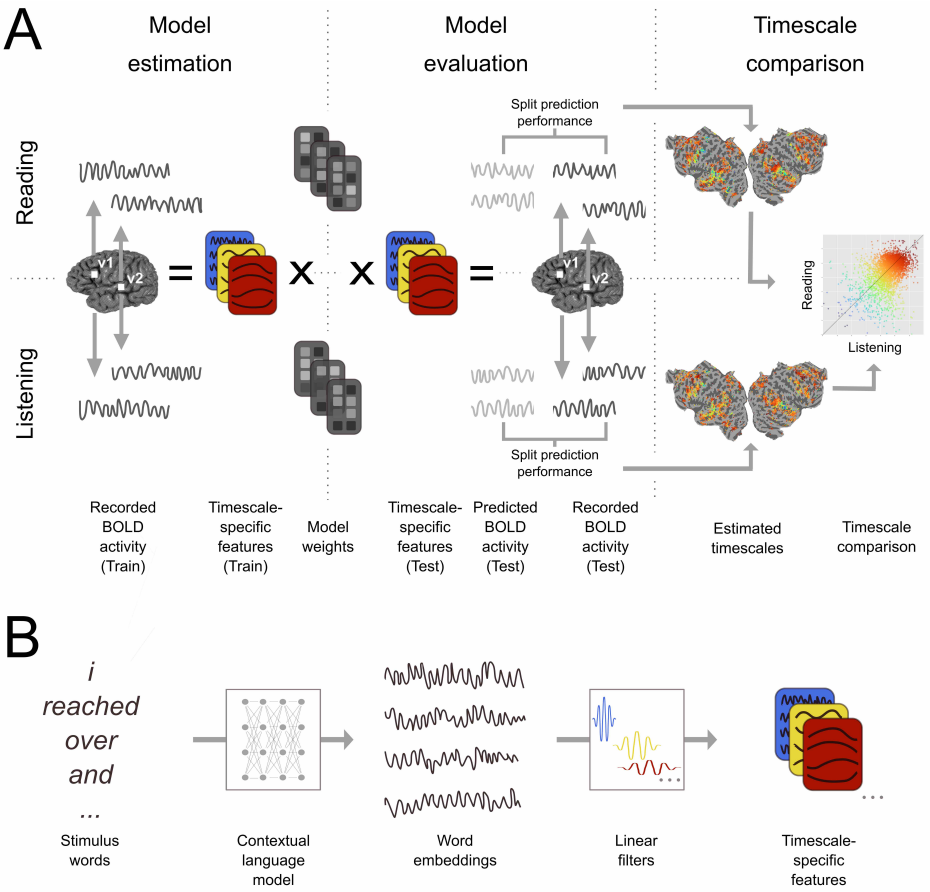

Figure 4: **Experimental procedure and voxelwise modeling.** The following procedure was used to compare the representation of different language timescales across the cerebral cortex. A. Functional MRI signals were recorded while participants listened to or read narrative stories (Huth et al., 2016; Deniz et al., 2019). Timescale-specific feature spaces were constructed, each of which reflects the components of the stimulus that occur at a specific timescale (See (B) for details). These feature spaces and BOLD activity were used to estimate a voxelwise encoding model that indicates how different language timescales modulate the BOLD signal evoked in each voxel, separately for each participant and modality ("Model estimation"). Estimated model weights were used to predict BOLD activity to a separate held-out dataset which was not used for model estimation ("Model evaluation"). Predictions for individual participants were computed separately for listening and reading sessions. Prediction performance was quantified as the correlation between the predicted and recorded BOLD activity to the held-out test dataset. This prediction performance was used to determine the selectivity of each voxel to language structure at each timescale. These estimates were then compared between reading and listening ("Timescale comparison"). B. Timescale-specific feature spaces were constructed from the presented stimuli. A contextual language model (BERT (Devlin et al., 2019)) was used to construct a vector embedding of the stimulus. The resulting stimulus embedding was decomposed into components at specific timescales. To perform this decomposition, the stimulus embedding was convolved across time with each of eight linear filters. Each linear filter was designed to extract components of the stimulus embedding that vary with a specific period. This convolution procedure resulted in eight sets of stimulus embeddings, each of which reflects the components of the stimulus narrative that vary at a specific timescale. These eight sets of stimulus embeddings were used as timescale-specific feature spaces in (A).

model describes how each feature space is represented in the activity of each voxel. A held-out dataset that was not used for model estimation is then used to evaluate model prediction performance on new stimuli and to determine the significance of the model prediction performance.

4.4.1 Construction of timescale-specific feature spaces

To operationalize the notion of language timescales, the language stimulus was treated as a time series and different language timescales were defined as the different frequency components of this time series. Although this operational definition is not explicitly formulated in terms of classic language abstractions such as sentences or narrative chains, the resulting components nonetheless selectively capture information corresponding to the broad timescales of words, sentences, and discourses (Tamkin et al., 2020). To construct timescale-specific feature spaces, first an artificial neural language model ("BERT" (Devlin et al., 2019)) was used to project the stimulus words onto a contextual word embedding space. This projection formed a stimulus embedding that reflects the language content in the stimuli. Then, linear filters were convolved with the stimulus embedding to extract components that each vary at specific timescales. These two steps are detailed in the following two paragraphs.

An artificial neural network (*BERT-base-uncased* (Devlin et al., 2019)) was used to construct the initial stimulus embedding. BERT-base is a contextual language model that contains a 768-unit embedding layer and 12 transformer layers, each with a 768-unit hidden state. (For additional details about the BERT-base model see Devlin et al. (2019).) The w words of each stimulus narrative X were tokenized and then provided one sentence at a time as input to the pretrained BERT-base model. For each stimulus word, the activation of each of the $p = 13 \times 768 = 9984$ units of BERT was used as a p-dimensional embedding of that word. The embeddings of the w stimulus words form a $p \times w$ stimulus embedding $M(X)$. $M(X)$ numerically represents the language content of the stimulus narratives. This stimulus embedding can explain a large proportion of the variance in brain responses to language stimuli (Toneva and Wehbe, 2019; Caucheteux and King, 2020; Schrimpf et al., 2020). However, this stimulus embedding does not distinguish between different language timescales.

In order to distinguish between different language timescales, linear filters were used to decompose the stimulus embedding $M(X)$ into different language timescales. Intuitively, the stimulus embedding consists of components that vary with different periods. Components that vary with different periods can be interpreted in terms of different classical language structures (Tamkin et al., 2020). For example, components that vary with a short period ($\sim$2-4 words) reflect clause-level structures such as syntactic complements, components that vary with an intermediate period ($\sim$16-32 words) reflect sentence-level structures such as constituency parses, and components that vary with a long period ($\sim$128-256 words) reflect paragraph-level structures such as semantic focus. To reflect this intuition, different language timescales were operationalized as the components of $M(X)$ with periods that fall within different ranges. The period ranges were chosen to be small enough to model timescale selectivity at a fine-grained temporal granularity and large enough to avoid substantial spectral leakage, which would contaminate the output of each filter with components outside the specified timescale. The predefined ranges were chosen as: 2-4 words, 4-8 words, 8-16 words, 16-32 words, 32-64 words, 64-128 words, 128-256 words, and 256+ words. To decompose the stimulus embedding into components that fall within these period ranges, eight linear filters b_i ($i \in 1, 2, .., 8$) were constructed. Each filter b_i was designed to extract components that vary with a period in the predefined range. The window method for filter design was used to construct each filter (Harris, 1978). Each linear filter was constructed by multiplying a cosine wave with a blackman window (Blackman and Tukey, 1958). The stimulus embedding $M(X)$ was convolved with each of the eight filters separately to produce eight filtered embeddings $M_i(X)$, $i \in 1, 2, ..., 8$, each with dimension $p \times w$. To avoid filter distortions at the beginning and end of the stimulus, a mirrored version of $M(X)$ was concatenated to the beginning and end of $M(X)$ before the filters were applied to $M(X)$. Each filtered embedding $M_i(X)$ contains the components of the stimulus embedding that vary at the timescale extracted by the i-th filter.

4.4.2 Construction of sensory-level feature spaces

Two sensory-level feature spaces were constructed in order to account for the effect of low-level sensory information on BOLD activity. One feature space represents low-level visual information. This feature space was constructed using a spatiotemporal Gabor pyramid that reflects the spatial and motion frequencies of the visual stimulus. (For details see Deniz et al. (2019), Nishimoto et al. (2011), and

Nakai et al. (2021).) The second feature space represents low-level auditory information. This feature space was constructed using a cochleogram model that reflects the spectral frequencies of the auditory stimulus. (For details see de Heer et al. (2017), Deniz et al. (2019), and Nakai et al. (2021)).

4.4.3 Stimulus downsampling

Feature spaces were downsampled in order to match the sampling rate of the fMRI recordings. The eight filtered timescale-specific embeddings $M_i(X)$ contain one sample for each word. Because word presentation rate of the stimuli is not uniform, directly downsampling the timescale-specific embeddings $M_i(X)$ would conflate long-timescale embeddings with the presentation word rate of the stimulus narratives (Jain et al., 2020). To avoid this problem, a Gaussian radial basis function (RBF) kernel was used to interpolate $M_i(X)$ in order to form intermediate signals $M_i'(X)$, following Jain et al. (2020). Each $M_i'(X)$ has a constant sampling rate of 25 samples per repetition time (TR). After this interpolation step, an anti-aliasing, 3-lobe Lanczos filter with cut-off frequency set to the fMRI Nyquist rate (0.25 Hz) was used to resample the intermediate signals $M_i'(X)$ to the middle timepoints of each of the n fMRI volumes. This procedure produced eight timescale-specific feature spaces $F_i(X)$, each of dimension $p \times n$. Each of these feature spaces contains the components of the stimulus embedding that vary at a specific timescale. These feature spaces are sampled at the sampling rate of the fMRI recordings. The sensory-level feature spaces were not sampled at the word presentation rate. Therefore Gaussian RBF interpolation was not applied to sensory-level feature spaces.

Before voxelwise modeling, each stimulus feature was truncated, z-scored, and delayed. Data for the first 10 TRs and the last 10 TRs of each scan were truncated to account for the 10 seconds of silence at the beginning and end of each scan and to account for non-stationarity in brain responses at the beginning and end of each scan. Then the stimulus features were each z-scored in order to account for z-scoring performed on the MRI data (For details see "MRI data collection"). In the z-scoring procedure, the value of each feature channel was separately normalized by subtracting the mean value of the feature channel across time and then dividing by the standard deviation of the feature channel across time. Lastly, finite impulse response (FIR) temporal filters were used to delay the features in order to model the hemodynamic response function of each voxel. The FIR filters were implemented by concatenating feature vectors that had been delayed by 2, 4, 6, and 8 seconds (following e.g., Huth et al. (2016), Deniz et al. (2019), and Nakai et al. (2021)). A separate FIR filter was fit for each feature, participant, and modality.

4.4.4 Voxelwise encoding model fitting

Voxelwise encoding models were estimated in order to determine which features are represented in each voxel. Each model consists of a set of regression weights that describes BOLD activity in a single voxel as a linear combination of the features in a particular feature space. The models for all feature spaces were jointly estimated in order to account for potential complementarity between feature spaces (Nunez-Elizalde et al., 2019; Dupré la Tour et al., 2022).

Regression weights were estimated using banded ridge regression (Nunez-Elizalde et al., 2019). Unlike standard ridge regression, which assigns the same regularization parameter to all feature spaces, banded ridge regression assigns a separate regularization hyperparameter to each feature space. Banded ridge regression thereby avoids biases in estimated model weights that could otherwise be caused by differences in feature space distributions. Mathematically, the m delayed feature spaces $F_i(X), i \in 1, 2, ..., m$ (each of dimension p) were concatenated to form a feature matrix $F'(X)$ (dimension $(m \times p) \times n$). Then banded ridge regression was used to estimate a mapping B (dimension $v \times (\sum_{i=1}^{f} p)$) from $F'(X)$ to the matrix of voxel responses Y (dimension $v \times n$). B is estimated according to $\hat{B} = \arg\min_B ||Y - BF'(X)||_2^2 + \lambda||CB||_2^2$. The diagonal matrix C of regularization hyperparameters for each feature space and each voxel is optimized over 10-fold cross-validation. See Section 4.4.5 for details.

4.4.5 Regularization hyperparameter selection

Data for the ten narratives in the training dataset were used to select regularization hyperparameters for banded ridge regression. 10-fold cross-validation was used to find the optimal regularization hyperparameters for each feature space and each voxel. Regularization hyperparameters were chosen

separately for each participant and modality. In each fold, data for nine of the ten narratives were used to estimate an encoding model and the tenth narrative was used to validate the model. The regularization hyperparameters for each feature space and voxel were selected as the hyperparameters that produced the minimum squared error (L2) loss between the predicted voxel responses and the recorded voxel responses ($\arg\min_{hyperparameters} ||\hat{y} - y||_2^2$). Evaluating k regularization hyperparameters for m feature spaces requires k^m iterations ($10^10 = 100,000,000$ model fits in our case). Therefore it would be impractical to conduct a grid search over all possible combinations of hyperparameters. Instead, a computationally efficient two-stage procedure was used to search for hyperparameters (Dupré la Tour et al., 2022). The first stage consisted of 1,000 iterations of a random hyperparameter search procedure (Bergstra and Bengio, 2012). 1000 normalized hyperparameter candidates were sampled from a dirichlet distribution and were then scaled by 10 log-spaced values ranging from 10^{-5} to 10^5. Then the voxels with the lowest 20% of the cross-validated L2 loss were selected for refinement in the second stage. The second stage consisted of 1,000 iterations of hyperparameter gradient descent (Bengio, 2000). This stage was used to refine the hyperparameters selected during the random search stage. This hyperparameter search was performed using the Himalaya Python package (Dupré la Tour et al., 2022).

4.4.6 Model estimation and evaluation

The selected regularization hyperparameters were used to estimate regression weights that map from the timescale-specific feature spaces to voxel BOLD activity. Regression weights were estimated separately for each voxel in each modality and participant. The test dataset was not used to select hyperparameters or to estimate regression weights. The joint prediction performance r of the combined feature spaces was computed per voxel as the Pearson correlation coefficient between the predicted voxel responses and the recorded voxel responses. The split-prediction performance $\tilde{r}$ was used to determine how much each feature space contributed to the joint prediction performance r. The split-prediction performance decomposes the joint prediction performance of all the feature spaces r into the contribution $\tilde{r}_i, i \in 1, 2, \ldots m$ of each feature space. The split-prediction performance is computed as $\tilde{r}_i = \frac{\sum_t \hat{Y}_i[t]Y[t]}{\sqrt{(\sum_t \hat{Y}[t]^2)(\sum_t Y[t]^2)}}$. (Further discussion of this metric can be found in St-Yves and Naselaris (2018) and Dupré la Tour et al. (2022)).

4.4.7 Language-selective voxel identification

The set of "language-selective voxels" was operationally defined as the set of voxels that are accurately predicted by any of the eight timescale-specific feature spaces. To identify this set of voxels, the split-prediction performance was used. The total contribution $\tilde{r}_{all_timescales}$ of the eight timescale-specific feature spaces to predicting the BOLD activity in each voxel was computed as the sum of the split-prediction performance for each of the eight timescales $\tilde{r}_{all_timescales} = \sum_{i=1}^{8} \tilde{r}_{timescale_i}$. The significance of $\tilde{r}_{all_timescales}$ was computed by a permutation test with 1000 iterations. At each permutation iteration, the timecourse of the held-out test dataset was permuted by blockwise shuffling. (Shuffling was performed in blocks of 10 TRs in order to account for autocorrelations in voxel responses (Deniz et al., 2019; Jain et al., 2020)). The permuted timecourse of voxel responses was used to produce a null estimate of $\tilde{r}_{all_timescales}$. These permutation iterations produced an empirical distribution of 1000 null estimates of $\tilde{r}_{all_timescales}$ for each voxel. This distribution of null values was used to obtain the p-value of $\tilde{r}_{all_timescales}$ for each voxel separately. A false discovery rate (FDR) procedure was used to correct the resulting p-values for multiple comparisons within each participant and modality (Benjamini and Hochberg, 1995). A low p-value indicates that the timescale-specific feature spaces significantly contributed to accurate predictions of BOLD activity in the joint model. Voxels with a one-sided FDR-corrected p-value of less than $\alpha = 0.05$ were identified as language-selective voxels. The set of language-selective voxels was identified separately for each participant and modality.

4.5 Voxel timescale selectivity estimation

The encoding model estimated for each voxel was used to determine voxel timescale selectivity, which reflects the average language timescale to which a voxel is selective. In order to compute timescale selectivity, first the timescale selectivity profile ($\tilde{r}'$) was computed. The timescale selectivity profile reflects the selectivity of each voxel to each of the eight timescale-specific feature spaces. This metric

is computed by normalizing the vector of split-prediction performances of the eight timescale-specific feature spaces to form a proper set of proportions: $\tilde{r}'_{timescale_i} = \frac{max(0,\tilde{r}_{timescale_i})}{\sum_{j=1}^{8} max(0,\tilde{r}_{timescale_j})}$.

Comparing each index of the timescale selectivity profile separately cannot distinguish between cases in which a voxel represents similar timescales between reading and listening (e.g., 2-4 words for reading and 4-8 words for listening) and cases in which a voxel represents very different timescales between the two modalities (e.g., 2-4 words for reading and 128-256 words for listening). Therefore, we computed the timescale selectivity $\bar{\mathbf{T}}$ for each voxel, which reflects the average timescale of language to which a voxel is selective. To compute voxel timescale selectivity, first the timescale t_i of each feature space $F_i(X)$ was defined as the center of the period range of the respective filter b_i: $t_i = (p_{i,low} + p_{i,high})/2$, where $(p_{i,low}, p_{i,high})$ indicates the upper and lower end of the period range for filter i. Then, timescale selectivity was defined as a weighted sum of each feature space log-timescale: $\bar{\mathbf{T}} = 2^{\sum_{i=1}^{8}(\tilde{r}'_i \log_2(t_i))}$. Timescale selectivity was computed separately for each voxel, participant, and modality.

4.6 Voxel timescale comparison

To compare timescale selectivity between modalities, the Pearson correlation coefficient was computed between timescale selectivity during reading and listening across the set of voxels that are language-selective in both modalities. The significance of this correlation was determined by a permutation test with 1000 iterations. At each iteration and for each modality separately, the timecourse of recorded voxel responses was shuffled. The timecourses were shuffled in blocks of 10 TRs in order to account for autocorrelations in voxel responses. The shuffled timecourses of recorded voxel responses were used to compute a null value for the timescale selectivity of each voxel for each modality separately. The null values of timescale selectivity were correlated between reading and listening to form an empirical null distribution. This null distribution was used to determine the p-value of the observed correlation between timescale selectivity during reading and listening. Significance was computed for each participant separately.

In addition, for each of the eight timescale separately the Pearson correlation coefficient was computed between selectivity to that timescale during reading and listening. This correlation was performed across the set of voxels that are language-selective in both modalities. The significance of the observed correlations were computed by an analogous permutation test. At each of 1000 iterations the timecourse of recorded voxel responses was shuffled and then the shuffled voxel responses were used to compute null values of the timescale selectivity profile. For each timescale-specific feature space separately, the null values of the timescale selectivity profile were used to compute an empirical null distribution for the correlation between selectivity to that feature space during reading and listening. These null distributions were used to determine the p-value of the observed correlations. Significance was computed for each participant and for each timescale-specific feature space separately.

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Author contributions: C.C. and F.D. conceptualized the experiment. F.D. collected the data. C.C., T.D.T., and F.D. developed the methodology and contributed to the analysis. C.C., T.D.T., J.L.G., D.K., and F.D. wrote the paper.

Data availability: This study made use of data originally collected for separate studies (Huth et al., 2016; de Heer et al., 2017; Deniz et al., 2019). The data can be accessed at `https://berkeley.app.box.com/v/Deniz-et-al-2019`.

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Supplementary information

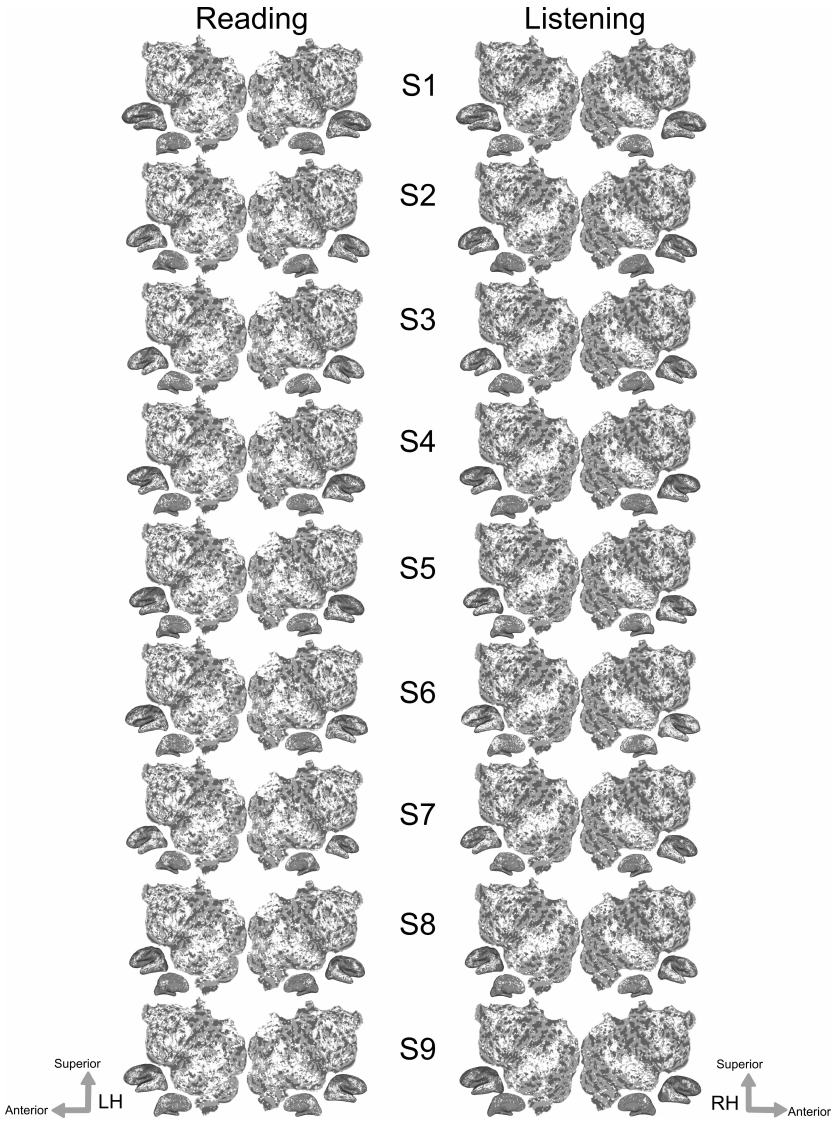

Figure 5: **Language-selective voxels in each modality.** The set of language-selective voxels is shown for reading and listening separately on the flattened cortical surface of each participant. Language-selective voxels are shown in white. For both modalities, voxels across temporal, parietal, and prefrontal cortices are language-selective.

	2-4 words	4-8 words	8-16 words	16-32 words	32-64 words	64-128 words	128-256 words	256+ words
S1	0.003*	<0.001*	0.004*	<0.001*	0.062	1	0.012*	0.001*
S2	<0.001*	<0.001*	<0.001*	<0.001*	0.048*	0.006*	0.038*	0.008*
S3	<0.001*	<0.001*	0.071	0.004*	0.039*	<0.001*	<0.001*	0.002*
S4	<0.001*	0.001*	0.008*	<0.001*	0.062	0.246	0.021*	0.005*
S5	<0.001*	<0.001*	0.563	0.001*	0.48	0.21	<0.001*	0.425
S6	<0.001*	<0.001*	0.001*	0.01*	0.658	0.043*	0.003*	0.043*
S7	<0.001*	<0.001*	<0.001*	0.092	0.088	0.001*	0.08	0.007*
S8	<0.001*	<0.001*	0.062	0.091	0.018*	0.157	0.003*	0.07
S9	<0.001*	<0.001*	0.001*	<0.001*	0.036*	<0.001*	<0.001*	<0.001*

Table 1: **Significance of correlation between selectivity to each timescale during reading and listening.** For each timescale, the Pearson correlation coefficient was computed across voxels between selectivity to that timescale during reading and listening in each separate participant (Figure 3). The p-value of each correlation is shown here. Asterisks indicate p-values that are significant (one-sided permutation test, $p < 0.05$, FDR corrected with a Benjamini-Hochberg correction for multiple comparisons).

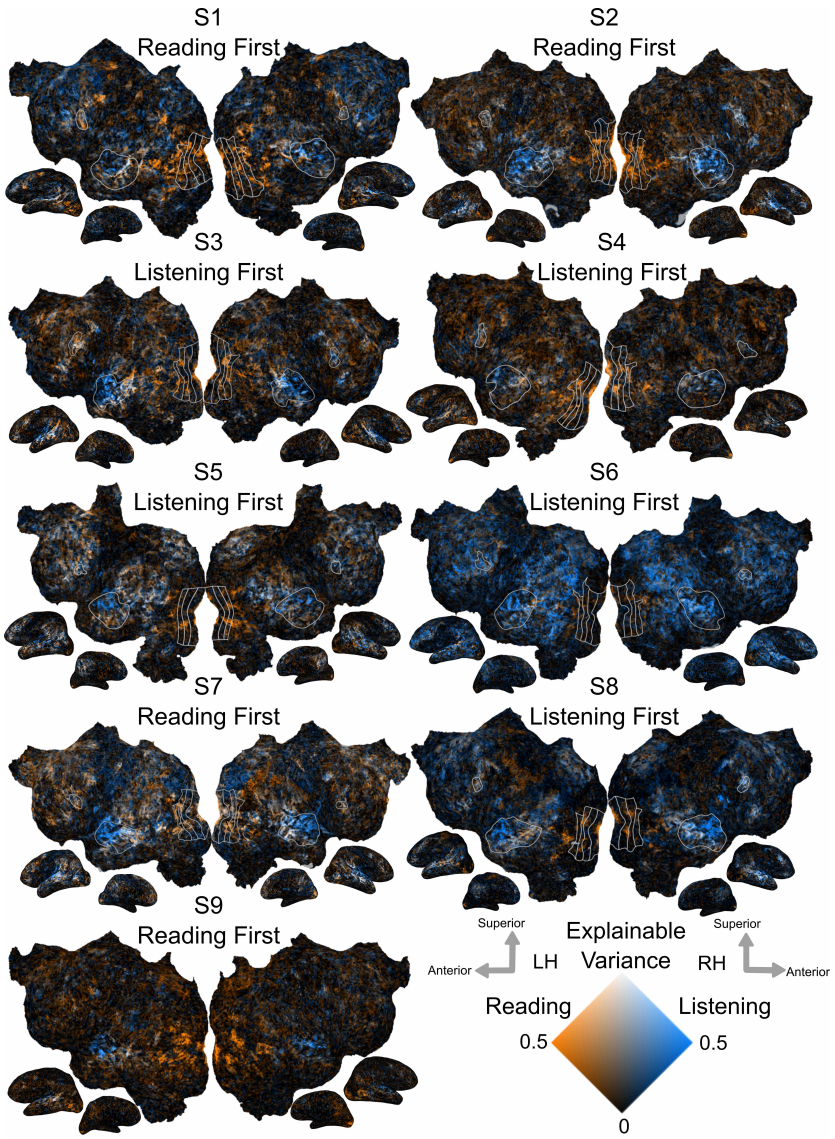

Figure 6: **Explainable variance in reading vs listening.** The difference in explainable variance (EV) between the reading and listening is shown on the flattened cortical surface of each participant. The first presented modality for each participant is indicated by the figure subtitles. Orange voxels had high EV for reading. Blue voxels had high EV for listening. White voxels had high EV for both modalities. The stimulus modality with stronger EV varies across participants, possibly due to individual participant preferences for certain modalities or because of small differences in noise across sessions.

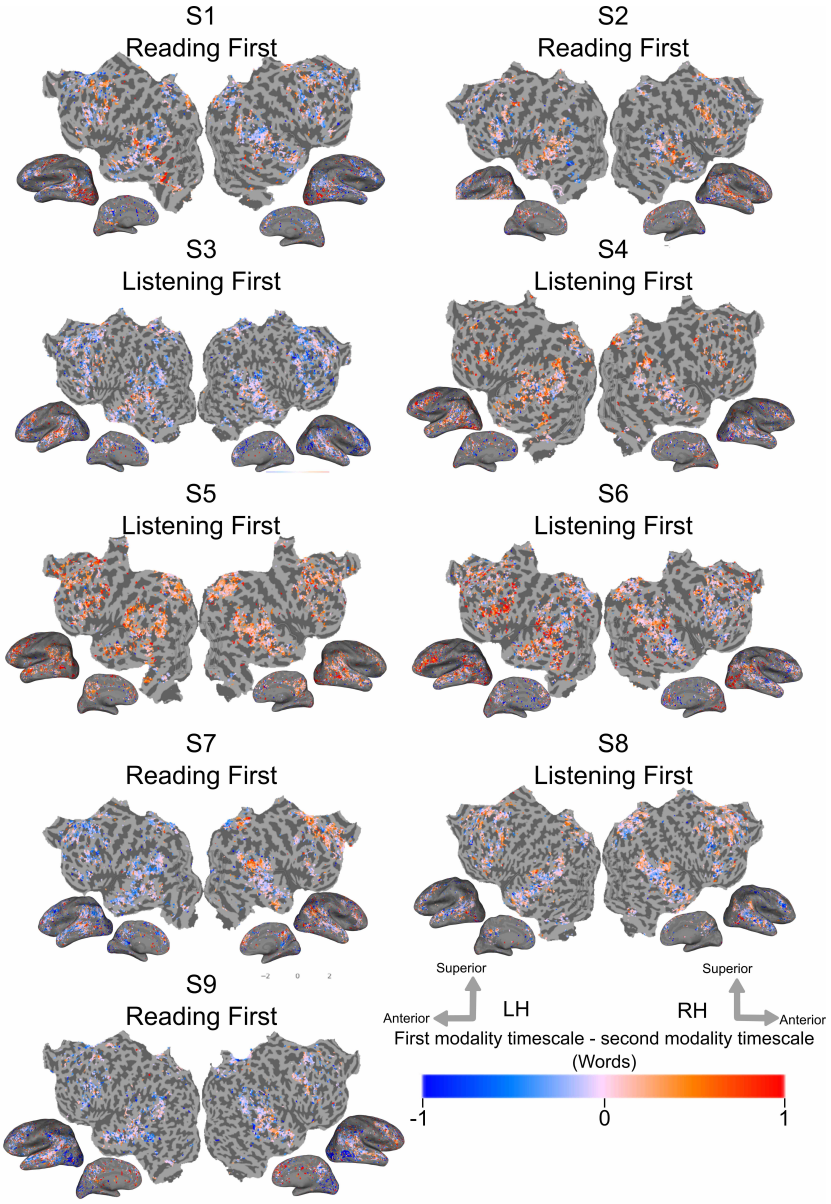

Figure 7: **Difference between timescale selectivity in first and second presented modalities.** The difference between timescale selectivity in the first and second presented modalities is shown on the flattened cortical surface of each participant. The first presented modality for each individual participant is indicated by the figure subtitles. Red voxels have longer timescale selectivity for the first presented modality. Blue voxels have longer timescale selectivity for the second presented modality. Voxels shown in grey were not significantly predicted in both modalities. Timescale selectivity was overall longer in the first presented modality than in the second presented modality in seven participants (S1, S2, S4, S5, S6, S8). Voxel timescale selectivity was on average longer in the second presented modality than in the first presented modality in the other two participants (S3, S7, S9).

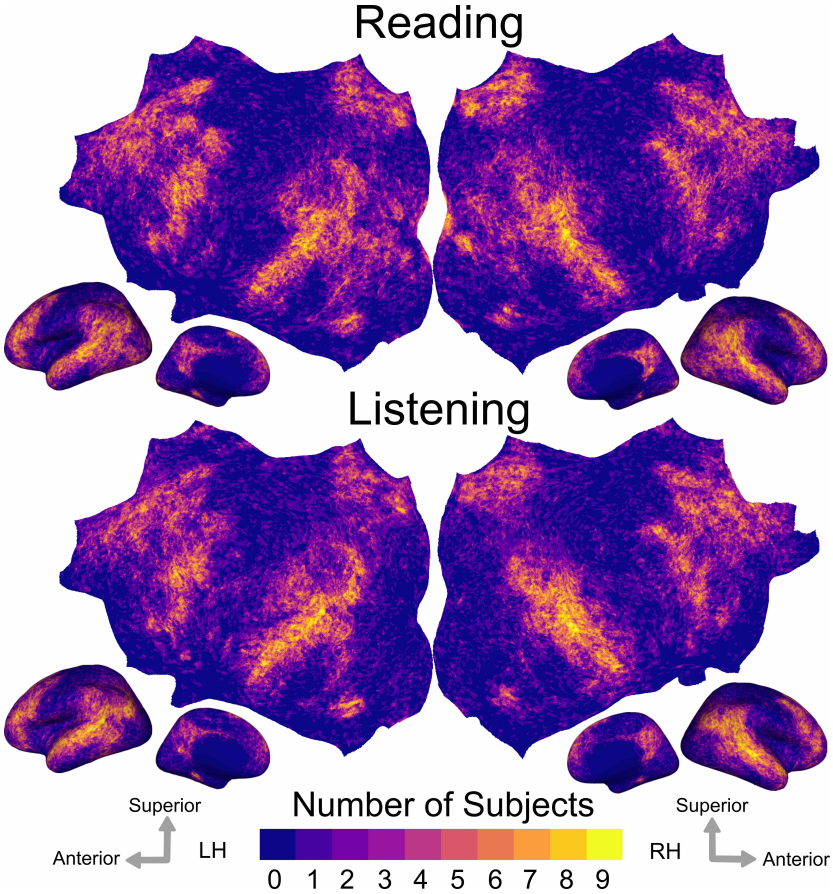

Figure 8: **Number of participants significantly predicted in each vertex.** The set of significantly predicted voxels in each participant was mapped to a standard fsaverage vertex space for reading and listening separately. The number of participants that was significantly predicted for each vertex is shown for reading (A) and listening (B) separately. The number of participants is indicated by the colorbar at the bottom. Brighter vertices are significantly predicted in more participants. Vertices across temporal, parietal, and prefrontal cortices are significantly predicted in most participants for both modalities.