Title: The extended language network: Language selective brain areas whose contributions to language remain to be discovered

Abbreviated title: The extended language network in the brain

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Abstract

Although language neuroscience has largely focused on 'core' left frontal and temporal brain areas and their right-hemisphere homotopes, numerous other areas—cortical, subcortical, and cerebellar—have been implicated in linguistic processing. However, these areas' contributions to language remain unclear given that the evidence for their recruitment comes from diverse paradigms, many of which conflate language processing with perceptual, motor, or task-related cognitive processes. Using fMRI data from 772 participants performing an extensively-validated language 'localizer' paradigm that isolates language processing from other processes, we a) delineate a comprehensive set of areas that respond reliably to language across written and auditory modalities, and b) evaluate these areas' selectivity for language relative to a demanding non-linguistic task. In line with prior claims, many areas outside the core fronto-temporal network respond during language processing, and most of them show selectivity for language relative to general task demands. These language-selective areas of the extended language network include areas around the temporal poles, in the medial frontal cortex, in the hippocampus, and in the cerebellum, among others. Although distributed across many parts of the brain, the extended language-selective network still only comprises ~1.2% of the brain's volume and is about the size of a strawberry, challenging the view that language processing is broadly distributed across the cortical surface. These newly identified language-selective areas can now be systematically characterized to decipher their contributions to language processing, including testing whether these contributions differ from those of the core language areas.

Significance statement

Language processing consistently recruits a left-lateralized fronto-temporal brain network, but language tasks often engage areas outside this core system. In an fMRI dataset of 772 participants performing a validated language localizer task, we identified 17 brain areas outside the core network that respond to both auditory and written language. Most of these areas show selectivity for language, including regions in the temporal poles, medial frontal cortex, hippocampus, and cerebellum. Despite its large number of components, this extended language network still only takes up ~1.2% of the brain's volume, challenging the view that language processing is broadly distributed in the brain. These findings lay the foundation for systematically characterizing these newly identified non-canonical language-selective areas.

Introduction

Language processing engages a left-lateralized fronto-temporal brain network—the "language network"—which selectively supports comprehension and production across modalities, including computations related to lexical access and combinatorial syntactic and semantic processing (reviews: Vigneau et al., 2006; Turker et al., 2023; Fedorenko et al., 2024). In addition to this 'core' network and its right-hemispheric homotopic regions (Lindell, 2006; Martin et al., 2022), several other brain structures have been implicated in aspects of language. In the cortex, such areas include medial frontal areas, especially in the pre-SMA (Bohsali & Crosson, 2016; Hertrich et al., 2016; Ardila, 2020), medial and lateral parietal areas (Hasson et al., 2007; Peschke et al., 2012; Papagno et al., 2017), temporal poles (Holland & Lambon Ralph, 2010; Lambon Ralph et al., 2017), ventral temporal areas (Krauss et al., 1996; Bédos Ulvin et al., 2017; Snyder et al., 2023), and even occipital areas in the blind (Bedny et al., 2011; Reich et al., 2011; Kim et al., 2017) but also sighted populations (Dikker et al., 2010, 2009; Seydell-Greenwald et al., 2023). Subcortically, language-implicated areas include the hippocampus (Piai et al., 2016; Dijksterhuis et al., 2024; reviews: Duff & Brown-Schmidt, 2012; Covington & Duff, 2016; Blank et al., 2016; Duff & Brown-Schmidt, 2017), the thalamus (Wahl et al., 2008; review: Klostermann & Ehlen, 2013), and basal ganglia structures, including the caudate, the pallidum, and the putamen (Crosson et al., 2003; Booth et al., 2007; Kotz et al., 2009; Oberhuber et al., 2013; Thibault et al., 2021). Finally, parts of the cerebellum have long been implicated in speech and language (reviews: Murdoch, 2010; Mariën et al., 2014; LeBel & D'Mello, 2023).

However, the precise contributions of these additional brain areas to language remain unclear. Much of the evidence comes from studies relying on single experimental paradigms, many of which fail to isolate language processing from perceptual or motor components, or from general task demands (for discussion, see Fedorenko et al., 2024). Another major limitation of past neuroimaging studies is the reliance on the group-averaging approach, which complicates across-study comparisons. In this approach, individual maps are averaged voxel-wise, and group-level activity peaks are reported in a standardized coordinate system (e.g., MNI; (Mazziotta et al., 2001). However, inter-individual anatomical variability leads to differences in structural and functional topographies (Frost & Goebel, 2012; Tahmasebi et al., 2012; Fedorenko, 2021; Michon et al., 2022), which may shift the group peaks across studies even for the same paradigm. Furthermore, any macro-anatomical structure encompasses multiple functionally distinct areas, making it difficult to unambiguously determine whether nearby peaks reported in different studies correspond to the same functional area (earlier discussions: Brett et al., 2002; Saxe et al., 2006).

One approach that circumvents these challenges is functional localization (Saxe et al., 2006; Kanwisher, 2010; Fedorenko, 2021). Instead of averaging brains together, this approach identifies functional areas within individuals using 'localizer' tasks—robust contrasts that target a particular perceptual or cognitive process. This approach ensures that functionally equivalent area(s) are referred to across individuals and studies, supporting the systematic

characterization of each area's responses across paradigms, as needed to understand its computations.

Here, we use an established language localizer and a large fMRI dataset to search for language-selective areas across the brain. In line with past claims, we find many areas outside the left fronto-temporal network that respond to language, and many of these areas show selectivity for language relative to a demanding non-linguistic cognitive task, which makes them exciting targets for future investigations.

Methods

Overview

We leverage a dataset of 772 participants who performed an extensively validated reading-based language localizer (Fedorenko et al., 2010). A fraction of these participants (n=86) additionally performed an auditory version of the language localizer (Malik-Moraleda, Ayyash et al., 2022), which allowed us to evaluate whether the observed language responses are robust to modality (reading vs. listening). If a brain region, akin to the core frontal and temporal language areas, responds to both written and auditory linguistic inputs (Fedorenko et al., 2010; Vagharchakian et al., 2012; Regev et al., 2013; Deniz et al., 2019), its computations plausibly have to do with the content of the linguistic signals rather than their surface (visual or auditory) properties. Finally, 422 of the participants also performed a demanding spatial working memory task, which allowed us to begin evaluating the selectivity of the areas in the extended language network. In all analyses, we define regions of interest functionally within individual participants; what varies across analyses is what group-level *masks* or *parcels* are used to constrain the selection of individual-level functional regions of interest (fROIs). In one approach, we use functional parcels derived from a group-level representation of the language localizer activity (Fedorenko et al., 2010). This approach identifies brain areas where most participants show a response to the target language contrast (at a specified whole-brain threshold). In a complementary approach, we use anatomical parcels from several commonly used brain atlases. The atlas-based approach can a) inform future language studies that rely on these atlases, by constraining them to particular subsets of areas, and b) can help identify language-responsive areas that may be missed by the other approach, thus providing a comprehensive evaluation of language responsiveness and selectivity in the brain. We describe both approaches in more detail next.

Approach 1*: Group-level parcels are derived directly from the language localizer data via Group-constrained Subject-Specific (GSS) parcellation.*

Fedorenko et al. (2010) developed an algorithmic method to determine which parts of the activation landscape are consistent across participants and to establish correspondences across individuals. This approach overlays thresholded, binarized individual maps for a particular contrast of interest in a common brain space to create a probabilistic activation overlap map. Subsequently, this map is divided into parcels using a watershed image parcellation algorithm (see Julian et al., 2012 for the application of this approach to the ventral visual stream areas).

Here, we used a set of 706 individual maps and selected the 20% most language-responsive voxels across the brain in each individual (Methods). This relatively liberal individual-subject threshold increases the likelihood of capturing all language-responsive areas, including those with weaker and less spatially consistent responses (see **Figure 1** in the OSF repository at https://osf.io/7594t/ for a visual comparison with parcels derived from a more conservative threshold – top 10% of the most language-responsive voxels across the brain).

Approach 2*: Group-level parcels are derived from existing anatomical and multi-modal atlases.*

To facilitate comparisons with other work, and to ensure that we are not missing any language-responsive areas with our first approach, we evaluated language responses in four standard brain atlases: 1) the Desikan-Killiany-Tourville atlas (Klein & Tourville, 2012), 2) the Harvard-Oxford Cortical atlas (Desikan et al., 2006), 3) the multi-modal Glasser atlas (Glasser et al., 2016), and 4) the Harvard-Oxford Subcortical atlas (Desikan et al., 2006). The first three atlases cover the cortical sheet, and the Harvard-Oxford Subcortical atlas covers the subcortical structures.

Across both approaches, to define subject-specific language fROIs, we intersect each subject's language localizer map with the relevant parcels and—within each parcel—select the 10% of voxels that show the strongest response to the localizer contrast (Methods).

Participants

772 neurotypical adults (age: mean=27, range=18-81; 438 females) participated in the experiments. 706 participants (age: mean=27, range=18-81; 404 females), all native speakers of English, performed the standard reading-based language localizer Fedorenko (Fedorenko et al., 2010). Twenty of the 706 native English speakers, along with 66 additional participants (native speakers of diverse languages and proficient English speakers)—a total of 86 participants (age: mean=28, range=19-45; 44 females)—performed an auditory language localizer task in their native language (data reported in Malik-Moraleda, Ayyash, et al., 2022), in addition to the reading localizer in English. Finally, a subset of 422 participants (age: mean=29, range=17-80, 225 females) performed the spatial working memory task (Fedorenko et al., 2013). All participants gave written informed consent, in accordance with the requirements of MIT's Committee on the Use of Humans as Experimental Subjects (COUHES) and were paid for their participation.

Tasks

As detailed below, we used three tasks (**Figure 1**): a standard reading-based language localizer (Fedorenko et al., 2010), an auditory language localizer based on excerpts from *Alice in Wonderland* (Malik-Moraleda, Ayyash, et al., 2022), and a spatial working memory task (Fedorenko et al., 2013; Assem et al., 2020).

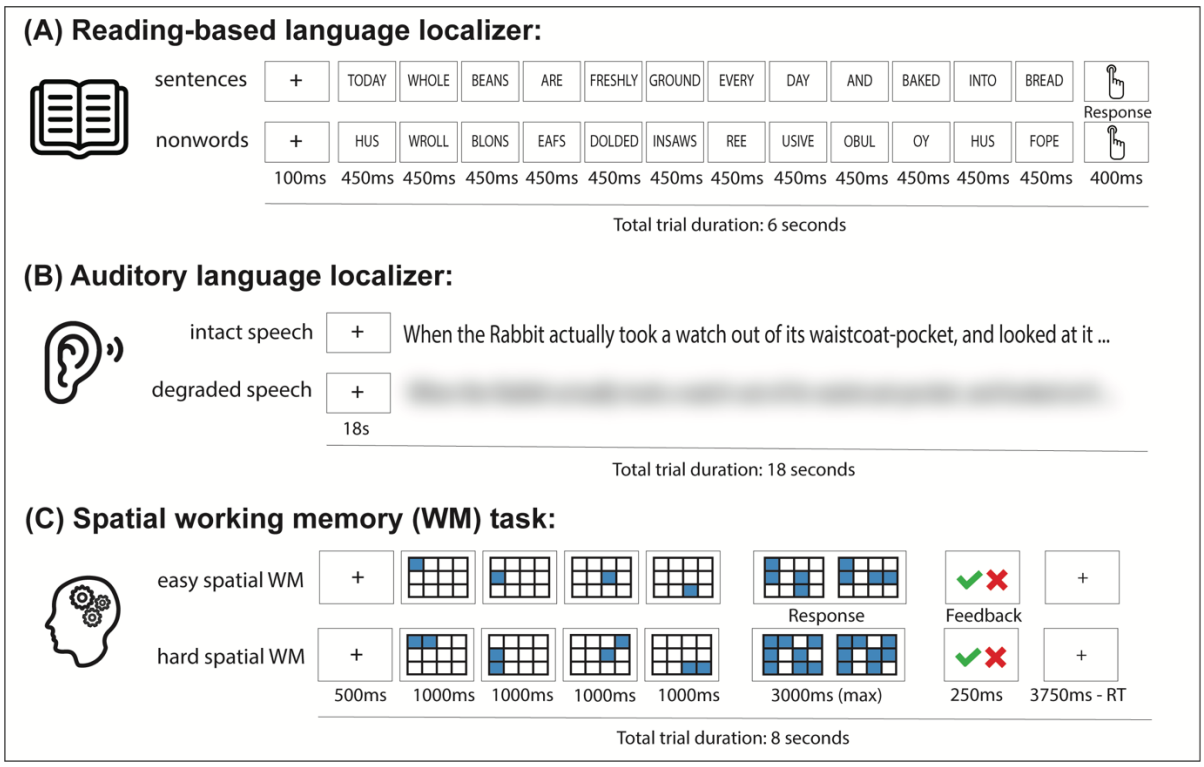

Figure 1. Overview of the three tasks. A sample trial in each condition for each task. Panel (A) presents the reading version of the language localizer, where sentences or lists of nonwords were presented one word/nonword at a time in the center of the screen at the rate of 450 ms, followed by a simple button press task. Trials in each condition were grouped into sets of 3 to make up experimental blocks. Panel (B) presents the auditory version of the language localizer, where an 18s-long recording of a passage from *Alice in Wonderland* or an acoustically degraded version of a passage was played while a fixation cross was displayed on the screen. Panel (C) presents the spatial working memory task, where a 3 x 4 grid was presented, and a sequence of squares flashed up within the grid (one at a time in the easy condition, or two at a time in the hard condition). Participants were asked to keep track of the square locations (4 or 8 in total in the easy and hard conditions, respectively) and, at the end of the trial, to choose a grid with the correct locations from two alternatives, followed by visual feedback. Trials in each condition were grouped into sets of 4 to make up experimental blocks.

Reading-based language localizer task

Participants passively read English sentences and lists of pronounceable nonwords, which appeared on the screen one word/nonword at a time (**Figure 1**). Each trial started with a 100 ms fixation, followed by a 12-element-long sequence of words/nonwords presented at the rate of 450 ms. At the end of each trial, a drawing of a hand appeared for 400 ms, and participants had to press a button every time they saw this drawing. The button press task was included to help the participants stay alert and focused during the task. Each trial ended with a blank screen presented for 100 ms. The task followed a blocked design. The total duration of each trial was 6 seconds, and 3 trials were included in each block. Each run included sixteen 18-second-long blocks (8 per condition). Additionally, five fixation blocks of 14 seconds were included in each run, for a total run duration of 358 seconds. Each participant completed two runs. The *Sentences > Nonwords* contrast targets brain areas that support language processing (including mental operations related to lexical retrieval, syntactic structure building, and semantic composition), while excluding perceptual processing.

Auditory language localizer task

Participants passively listened to both intact and acoustically degraded passages from *Alice in Wonderland* (Carroll, 1865; **Figure 1**). The degraded condition was created based on the original passages but sounded like poor radio reception, with preserved prosody but without decipherable words or phonemes (see Malik-Moraleda, Ayyash, et al., 2022 for details of stimulus creation). Each trial consisted of an 18-second recording. Each run included 12 18-second-long trials (4 per condition; in addition to the intact and degraded conditions, the experiment included a third condition not included in any analyses here—recordings in an unfamiliar foreign language). Additionally, three fixation blocks of 12 seconds were included in each run, for a total run duration of 252 seconds. Each participant completed three runs. As in the reading-based localizer, the *Intact* > *Degraded* contrast targets brain areas that support language processing.

A demanding non-linguistic (spatial working memory) task

Participants performed a spatial working memory task consisting of easier and harder trials (e.g., Fedorenko et al., 2013; Assem et al., 2020). Each trial started with a 500 ms fixation. Then, a 3 x 4 grid appeared in the center of the screen, and a series of locations were flashed in blue at the rate of 1 second per flash (**Figure 1**). In the easy condition, one location flashed at a time (four locations in total); in the hard condition, two locations flashed at a time (eight in total). Participants were instructed to keep track of the locations. Each trial ended with a two-choice forced choice task: two grids with different sets of locations were shown side by side, and participants had to choose the grid that shows the locations just presented. They were told whether they chose correctly (green checkmark) or not (red cross). The task followed a blocked design. The total duration of each trial was 8 seconds, and 4 trials were included in each block. Each run included ten 32-second-long blocks (5 per condition). Additionally, six fixation blocks of 16 seconds were included in each run, for a total run duration of 448 seconds. Each participant completed 2 runs. The *Hard* > *Easy* contrast targets brain areas that support demanding cognitive tasks, including mental operations associated with working memory, attention, and cognitive control.

fMRI data acquisition

Structural and functional data collected in the Athinoula A. Martinos Imaging Center at the McGovern Institute for Brain Research at MIT. Structural and functional data were acquired using a Siemens Trio 3 Tesla scanner before or after a Prisma upgrade (n=508 and n=264, respectively) and a 32-channel head coil. High-resolution, whole-brain anatomical images were acquired using two different T1-weighted MPRAGE sequence (**Sequence 1**: n=508, 176 sagittal slices; voxel size 1 x 1 x 1 mm^3; TR = 2530 ms, TE = 3.48 ms, flip angle = 9°; **Sequence 2**: n=264, 208 sagittal slices; voxel size 0.9 x 0.9 x 0.9 mm^3; TR = 1800 ms, TE = 2.40 ms, flip angle = 9°). Functional T2*-weighted images were acquired using three different whole-brain echo-planar (EPI) pulse sequences with phase encoding direction A >> P (**Sequence 1, Siemens Trio**: n = 508, 31 near-axial slices, 2.1 × 2.1 × 4 mm voxels; TR = 2,000 ms; TE = 30 ms; flip angle = 90°; matrix size 96 x 96 mm; MB acceleration factor 0; **Sequence 2,**

Siemens Prisma: n = 73, 52 near-axial slices, 2 × 2 × 2 mm isotropic voxels; TR = 2,000 ms; TE = 30 ms; flip angle = 90°; matrix size 104 x 104 mm; MB acceleration factor 2; **Sequence 3, Siemens Prisma**: n = 191, 72 near-axial slices, 2 × 2 × 2 mm isotropic voxels; TR = 2,000 ms; TE = 30 ms; flip angle = 90°; matrix size 104 x 104 mm; MB acceleration factor 3). The first 10 s of each run were excluded to allow for steady state magnetization.

fMRI data preprocessing

fMRI data were analyzed using SPM12 (release 7487), CONN EvLab module (release 19b), and other custom MATLAB scripts. Each participant's functional and structural data were converted from DICOM to NIFTI format. All functional scans were coregistered and resampled using 4th degree B-spline interpolation to the first scan of the first session (Friston et al., 1995). Potential outlier scans were identified from the resulting subject-motion estimates as well as from BOLD signal indicators using default thresholds in CONN preprocessing pipeline (5 standard deviations above the mean in global BOLD signal change, or framewise displacement values above 0.9 mm; Nieto-Castañón, 2020). Functional and structural data were independently normalized into a common space (the Montreal Neurological Institute [MNI] template; IXI549Space) using SPM12 unified segmentation and normalization procedure (Ashburner & Friston, 2005) with a reference functional image computed as the mean functional data after realignment across all timepoints omitting outlier scans. The output data were resampled to a common bounding box between MNI-space coordinates (-90, -126, -72) and (90, 90, 108), using 2mm isotropic voxels and 4th degree B-spline interpolation for the functional data, and 1mm isotropic voxels and trilinear interpolation for the structural data. Last, the functional data were smoothed spatially using spatial convolution with a 4 mm FWHM Gaussian kernel.

fMRI data first-level modeling

Responses in individual voxels were estimated using a General Linear Model (GLM) in which each experimental condition was modeled with a boxcar function convolved with the canonical hemodynamic response function (HRF) (fixation was modeled implicitly). Temporal autocorrelations in the BOLD signal timeseries were accounted for by a combination of high-pass filtering with a 128 seconds cutoff, and whitening using an AR(0.2) model (first-order autoregressive model linearized around the coefficient a=0.2) to approximate the observed covariance of the functional data in the context of Restricted Maximum Likelihood estimation (ReML). In addition to experimental condition effects, the GLM design included first-order temporal derivatives for each condition (included to model variability in the HRF delays), as well as nuisance regressors to control for the effect of slow linear drifts, subject-specific motion parameters (6 parameters), and potential outlier scans (identified during preprocessing as described above) on the BOLD signal.

Creation of group-level language parcels

The group-level functional parcels were created using the group-constrained subject-specific approach (GSS; Fedorenko et al., 2010) as implemented in the spm_ss toolbox (available for

download from: https://www.evlab.mit.edu/resources). This approach creates a parcellation based on the functional data and relies on a probabilistic activation overlap map created from individual subjects' activation maps to represent areas of spatially consistent (across participants) activations in response to a given task. In the ***first step***, individual maps for the relevant contrast (here, the *Sentences > Nonwords* contrast from the reading-based language localizer) were thresholded to only include the 20% of voxels with the highest contrast values. As noted above, we used a relatively liberal threshold to include areas that may respond reliably but weakly to language, but the average t-value across participants for these voxels was still quite high: 2.02 (SD=0.6; average min t-value: 0.92, average max t-value: 14.17). These maps were then binarized (i.e., any voxel exceeding the threshold was assigned a value of 1, and the remaining voxels were assigned a value of 0). In the ***second step***, the 706 individual binarized maps were overlaid in a common space, creating a probabilistic activation overlap map. In this map, the value of each voxel, divided by the total number of participants, represents the proportion of participants for whom that voxel belongs to the top 20% of most language-responsive voxels (the highest value in this map is ~0.78, in line with Lipkin et al., 2022). The map was then thresholded to remove voxels with values below 0.1 (i.e., voxels present in fewer than 10%, or 71 of the 706 participants) and smoothed with a 6 mm full-width half-maximum Gaussian kernel, to avoid over-parcellation. In the ***third step***, the probabilistic map was divided into parcels using an image segmentation (watershed) algorithm (Meyer 1991), which seeks to identify the main "hills" in the activation landscape. In our dataset, this algorithm identified 33 parcels. Six parcels that were smaller than 150 voxels in size were excluded from further analyses, leaving the final set of 27 parcels: 11 in the left hemisphere, 8 in the right hemisphere, 3 midline bilateral parcels, and 5 parcels in the cerebellum (**Figure 3** and **Table 1**).

Estimation of response to the three tasks in the individual fROIs (constrained by the functional or anatomical parcels)

We defined language-responsive fROIs using five sets of parcels: the functional parcels (created as described above) and four sets of anatomical parcels: 1) the Desikan-Killiany-Tourville atlas (Klein & Tourville, 2012), 2) the Harvard-Oxford Cortical atlas (Desikan et al., 2006), and 3) the multi-modal Glasser atlas (Glasser et al., 2016), and 4) the Harvard-Oxford Subcortical atlas (Desikan et al., 2006) (see **SI Figure S1** for information on the overlap between the functional and anatomical parcels). Within each parcel, we defined a subject-specific functional ROIs (fROI) by selecting the top 10% of voxels showing the strongest response to the language localizer contrast (*Sentences > Nonwords*). Subsequently, we estimated the responses in these fROIs to the conditions of the auditory language localizer (*Intact speech* and *Degraded speech*) and the spatial working memory task (*Hard spatial WM* and *Easy spatial WM*). To estimate the responses to the *Sentences* and *Nonwords* conditions, we relied on an across-runs cross-validation procedure, which ensures that different subsets of the data are used for fROI definition and response estimation (e.g., Kriegeskorte et al., 2010).

Figure 2A schematically illustrates the procedure for defining individual-level fROIs, using the parcels based on the Glasser atlas. **Figure 2B** further demonstrates the benefits of individual-level fROIs relative to group-level parcels, where all voxels in the parcel are used

for each participant. As documented previously (e.g., Saxe et al., 2006; Fedorenko et al., 2012a; Nieto-Castañón & Fedorenko, 2012), group-level ROIs underestimate effect sizes and selectivity, and—for the frontal parcel—fail to distinguish between nearby functionally distinct areas, leading to apparent mixed selectivity (Fedorenko et al., 2012b; see Fedorenko & Blank, 2020 for discussion).

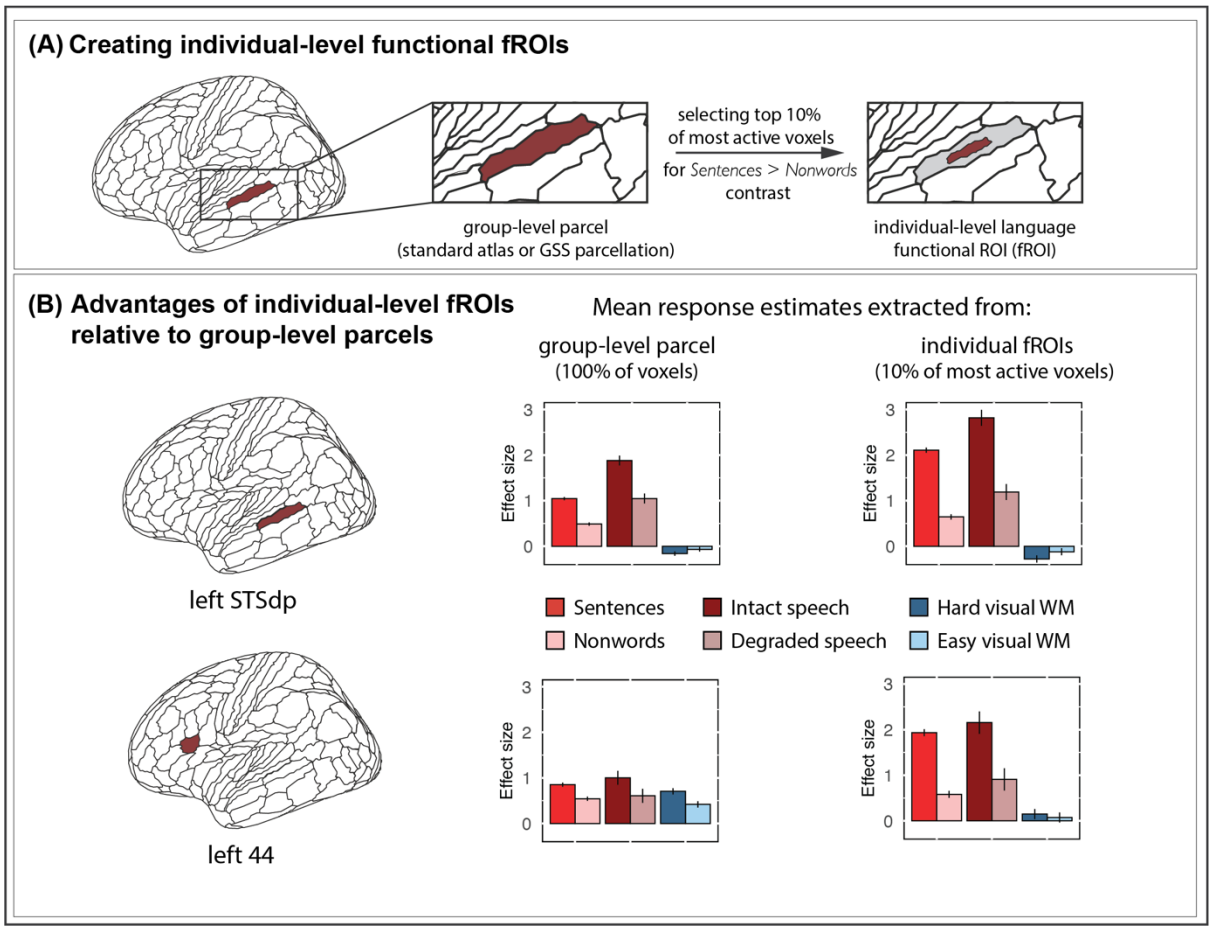

Figure 2. Definition of individual-level fROIs and their advantages over the group-level anatomical parcels. Panel (A) schematically shows how fROIs are created: here a parcel from the Glasser atlas (left STSdp) is used for illustration, but the procedure is the same for other parcels, including the parcels derived from the GSS procedure (Methods). Within each parcel, we select 10% of voxels showing the strongest response to the language localizer contrast (i.e., *Sentences* > *Nonwords*) using half of the data to ensure independence in estimating the fROIs' response profiles. Panel (B) demonstrates the advantage of individual-level fROIs for two sample parcels (left STSdp and left 44; both show high overlap with the probabilistic atlas of the language network; Lipkin et al., 2022): the bar graphs on the left show responses to the three tasks when all the voxels within the parcel are used for each participant, and the bar graphs on the right show responses in the individual-level fROIs (custom sets of 10% of voxels selected based on individual localizer activation maps). The individual fROIs show stronger and more selective responses (the responses to the *Sentences* and *Nonwords* conditions are estimated using an independent portion of the data).

Statistical analyses

The data were analyzed using linear mixed-effect models as implemented in the lmerTest package in R (Kuznetsova et al., 2017). We ran a separate analysis for each fROI in each of the five sets of fROIs (the five sets were defined using the five sets of parcels; Methods: Overview)

comparing the critical and baseline conditions in each task: the reading-based language localizer, the auditory language localizer, and the spatial working memory task using the following formula:

$$\text{EffectSize} \sim 1 + \text{Condition} * \text{Task} + (1 \mid \text{Subject})$$

The categorical predictor of *Condition* was deviation-coded using the treatment contrast which specified the control condition of each task as the baseline (the reading-based language localizer: *Sentences* = 1, *Nonwords* = 0; the auditory language localizer: *Intact speech* = 1, *Degraded speech* = 0; the spatial WM task: *Hard WM* = 1, *Easy WM* = 0). The categorical predictor of *Task* was deviation-coded using the treatment contrast and specifying the reading language localizer as the baseline.

Subsequently, we ran three post-hoc pairwise comparisons to test (i) differences between the critical and control conditions for each task (i.e., *Sentences* > *Nonwords*, *Intact* > *Degraded speech*, and *Hard WM* > *Easy WM*); (ii) whether in each task the responses to the critical and control conditions significantly differed from 0 (e.g., *Sentences* > *0* and *Nonwords* > *0* in the reading language task); and (iii) whether the responses to the critical condition significantly differed between a) each of the two language conditions (i.e., *Sentences* > *Intact speech*) and b) the non-linguistic Hard WM condition (i.e., *Sentences* > *Hard WM*, and *Intact speech* > *Hard WM*).

Code accessibility

All data, including 3d brain contrast maps, parcels, and data produced by the functional localization analysis toolbox (spm_ss) as well as the code necessary to replicate all analyses and plots presented in this paper is available at: https://osf.io/7594t/.

Results

We considered a region to contain a fROI **responsive to language** if the following conditions were met: 1) the response to both of the language contrasts (*Sentences* > *Nonwords* and *Intact* > *Degraded speech*) is positive and significant ($p<0.05$), and 2) the response to both of the critical conditions (i.e., *Sentences* for the reading language localizer and *Intact speech* for the auditory language localizer) falls significantly above the fixation baseline. We further considered a region to contain a fROI **selective for language** if, in addition to the abovementioned conditions, the critical language conditions (*Sentences* or *Intact speech*) elicited a reliably greater response than the critical condition for the non-linguistic task (i.e., *Hard WM*). Note that we do not apply a correction for multiple comparisons (regions) here because we are asking an independent question for each region (rather than asking whether the effect holds in *any* of the regions). Besides, the approach already has internal replicability "checks" built into it, including an across-runs cross-validation procedure for the reading-based contrast and generalization to the auditory language contrast. That said, most of the critical effects would survive a correction for the number of regions given the large sample size.

The extended set of language-selective regions discovered via the group-constrained subject-specific approach

Twenty-two of the 27 parcels identified by the whole-brain GSS analysis (Methods) contained fROIs that responded to language across modalities, with the exception of the three parcels in the occipital cortex, the parcel in the left precuneus / posterior ACC, and the parcel in the left parahippocampal gyrus (the fROIs in these parcels either did not show a significant response to one of the language contrasts or responded at or below baseline to one or both of the critical language conditions). Of the 22 language-responsive regions, 20 showed selective responses to language with little or no response to the demanding non-linguistic task; both of the exceptions were located in the cerebellum (**Figure 3**, **Table 1**; see **SI Table S1** for the details of the statistical tests). Note that in addition to these language-selective areas, most of these parcels contain areas that respond strongly to the non-linguistic task and not to the language tasks (see **SI Figure S2** and **S3**), in line with past evidence that distinct functional areas often lie near each other within the same anatomical structure (e.g., Fedorenko et al., 2012b; Braga et al., 2020)—a finding that reinforces the importance of functionally defining the relevant portion of each region within each individual. In addition to the core left lateral frontal and lateral temporal regions and their right-hemisphere homotopic regions, the extended language-selective network included regions in the bilateral temporal pole, in the left 'basal temporal language area' (BTLA; Lüders et al., 1986 see Li et al., 2024 for concortant evidence using a similar functional localization approach to the one used here) in the left precuneus, three regions in the medial frontal cortex (spanning different sections of the SFG and the frontal pole), and three cerebellar regions (left Crus II / VIIb, right Crus I / II / VIIb, and right VIIb / VIIIa in the cerebellum; see Casto et al., 2025 for concordant evidence).

It is important to note that even with these additional language-selective regions, language-selective cortex takes up a relatively small amount of total brain volume. Although the parcels (**Figure 3**) are, by design, large (to capture inter-individual variability in the precise locations of functional areas), the individual fROIs constitute only 10% of each parcel (Methods), for a total average volume of 25.1 cm^3 across the 20 language-selective regions. The volume is similar if instead of the top 10% of voxels, in each parcel we select voxels that show a significant ($p<0.001$) *Sentences>Nonwords* effect: 22.1 cm^3 on average (SD=12.8 cm^3), which is similar in size to a large strawberry, and takes up only ~1.21% of the whole brain volume (we take the brain volume to be 1,827.86 cm^3, which corresponds to the volume of non-zero voxels in the MNI152_T1_2mm_brain_mask–a standard template distributed in FSL). An average of 15.2 cm^3 (SD=8.2 cm^3) is taken up by the five core left-hemisphere fROIs (defined within the following parcels: AntTemp, PostTemp, IFGorb, IFG, and MFG), and 3.6 cm^3 (SD=3.7 cm^3)—by their right-hemisphere homotopes.

The full set of 27 parcels, in both the MNI and the fsaverage spaces, is available in an OSF repository (https://osf.io/7594t/; note that the fsaverage version was created by converting the volumetric set to the fsaverage space, not based on statistical maps generated in a surface space). Additionally, for the 20 parcels containing language-selective fROIs, we created a left-right symmetrical version, where the left-hemisphere cortical parcels were mirrored onto the

right hemisphere (the medial parcels were first split along the brain midline (x = 45)), and the right-hemisphere cerebellar parcels were mirrored onto the left hemisphere. This symmetrical set (also available at OSF repository at https://osf.io/7594t/ and at https://evlab.mit.edu/parcels) may be useful for defining the language fROIs in atypically lateralized (right-lateralized or bilateral) participants, or for directly comparing the profiles of the left- and right-hemisphere language regions. We also provide a left-right symmetrical version that uses—for the core areas—the parcels derived from a smaller set of participants and used in much past work (e.g., Diachek, Blank, Siegelman, et al., 2020; Ivanova et al., 2020; Shain et al., 2020; Schrimpf et al., 2021; Malik-Moraleda, Ayyash, et al., 2022).

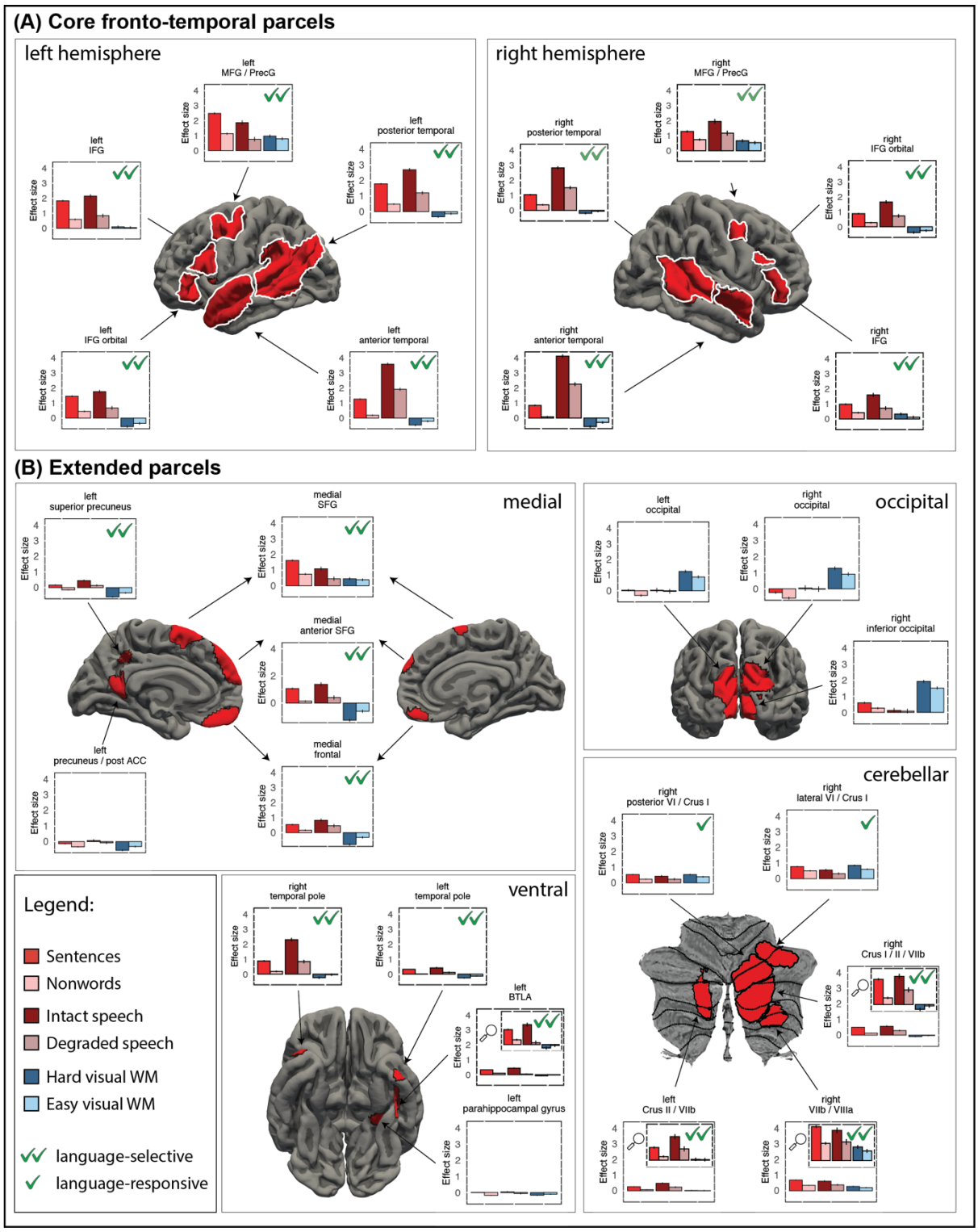

Figure 3. Language responsiveness and selectivity of the fROIs within the new, extended set of language parcels. The figure shows the surface projections of the cortical and cerebellar parcels (all the analyses were performed in the volume space, as described in Methods; the surface projections were created using FreeSurfer for the cortical and SUIT for the cerebellar parcels and are only used for visualization). Panel (A) shows the five core left-hemisphere parcels and their right-hemisphere homotopes; these parcels are additionally highlighted with white outlines. Panel (B) shows the extended set of parcels identified by the GSS procedure. Separate sub-panels show the medial, occipital, ventral, and cerebellar views of these parcels. For each region (defined based on individual activation maps, as described in Methods), we show responses to the reading-based and auditory language localizers (red bars; darker bars correspond to the critical conditions) and the non-linguistic spatial

working memory task (blue bars; the darker bar corresponds to the harder condition). For the reading-based localizer, the responses were estimated using independent runs of the data from the data used for the fROI definition. Parcels that contain language-responsive fROIs have a green checkmark in the upper right-hand corner; the ones where the fROIs are additionally language-selective have two green checkmarks. We used the same range of values for the y-axis across all regions to highlight differences in response magnitudes, but for the language-selective regions with low responses, we include insets, marked with a magnifying glass, where we restrict the y-axis to make the profiles easier to see.

Table 1. Functional language parcels. The 27 parcels yielded by the whole-brain group-constrained subject-specific approach (Methods). The parcel sizes are reported in cm^3 and the number of voxels (2x2x2 mm resolution); individual fROIs are 10% of the parcel size. As described in Methods, the subject-specific fROIs are defined as the top 10% of most language-responsive voxels in each parcel. The remaining two columns mark the parcels that contain language-responsive and language-selective fROIs (see Results for definitions).

Hemisphere	Name	Size (cm^3)	Size (n voxels)	Language-responsive	Language-selective
		Core frontal and temporal parcels			
left	IFG orbital	12,40	1550	✓	✓
left	IFG	16,71	2089	✓	✓
left	MFG / PrecG	18,79	2349	✓	✓
left	anterior temporal	32,52	4065	✓	✓
left	posterior temporal	52,99	6624	✓	✓
right	IFG orbital	7,13	891	✓	✓
right	IFG	5,89	736	✓	✓
right	MFG / PrecG	5,90	737	✓	✓
right	anterior temporal	12,30	1538	✓	✓
right	posterior temporal	25,01	3126	✓	✓
		Extended parcels			
left	temporal pole	1,64	205	✓	✓
left	BTLA	1,37	171	✓	✓
left	parahippocampal gyrus	1,27	159		
left	superior precuneus	2,42	302	✓	✓
left	precuneus / post ACC	4,30	538		
left	occipital	21,83	2729		
right	temporal pole	6,30	788	✓	✓
right	occipital	7,50	937		
right	inferior occipital	13,29	1661		
bilateral	medial frontal cortex	6,01	751	✓	✓
bilateral	medial anterior SFG	13,96	1745	✓	✓
bilateral	medial SFG	13,85	1731	✓	✓
left	Crus II / VIIb	3,00	375	✓	✓
right	Crus I / II / VIIb	9,20	1150	✓	✓
right	VIIb / VIIIa	3,60	450	✓	✓
right	posterior VI / Crus I	3,92	490	✓	

right	lateral VI / Crus I	3,05	381	✓

Language-selective regions in four standard brain atlases

To facilitate comparisons with other work, and to ensure that we are not missing any language-responsive areas, we evaluated language responses in four standard brain atlases: three cortical and one subcortical. Within each atlas, individual-level fROIs were defined in each parcel in the same way as for the functional parcels (i.e., by selecting the top 10% of most active voxels based on the reading localizer contrast).

Language-selective regions in the cortical atlases

In the DKT atlas, 20 of the 72 parcels contained language-selective fROIs: 13 in the left hemisphere and 7 in the right hemisphere. In the Harvard-Oxford Cortical atlas, 42 of the 96 parcels contained language-selective fROIs: 26 in the left hemisphere and 16 in the right hemisphere. Finally, in the Glasser multimodal atlas, 94 of the 380 parcels contained language-selective fROIs: 64 in the left hemisphere and 30 in the right hemisphere (five of these parcels did not show spatial overlap with any of the GSS parcels, and further 4 showed overlap lower than 10% - for their functional profiles see **Figure S4**). Across all three atlases, the parcels containing language-selective fROIs spanned bilateral frontal and temporal areas, as well as pre-central frontal and inferior parietal areas in the left hemisphere. Parcels that contain language-responsive and language-selective fROIs are presented in **Figure 3A** (see **Table 2** for the full list of language-responsive and language-selective regions). The functional profiles for all the left lateral regions—including the responses to the reading and auditory language localizers, and the non-linguistic spatial working memory task—are presented in **Figure 4B** (for a similar figure presenting all 4 views see **SI Figure S5;** details of the statistical tests can be found in **Table 1** in the OSF repository at https://osf.io/7594t/).

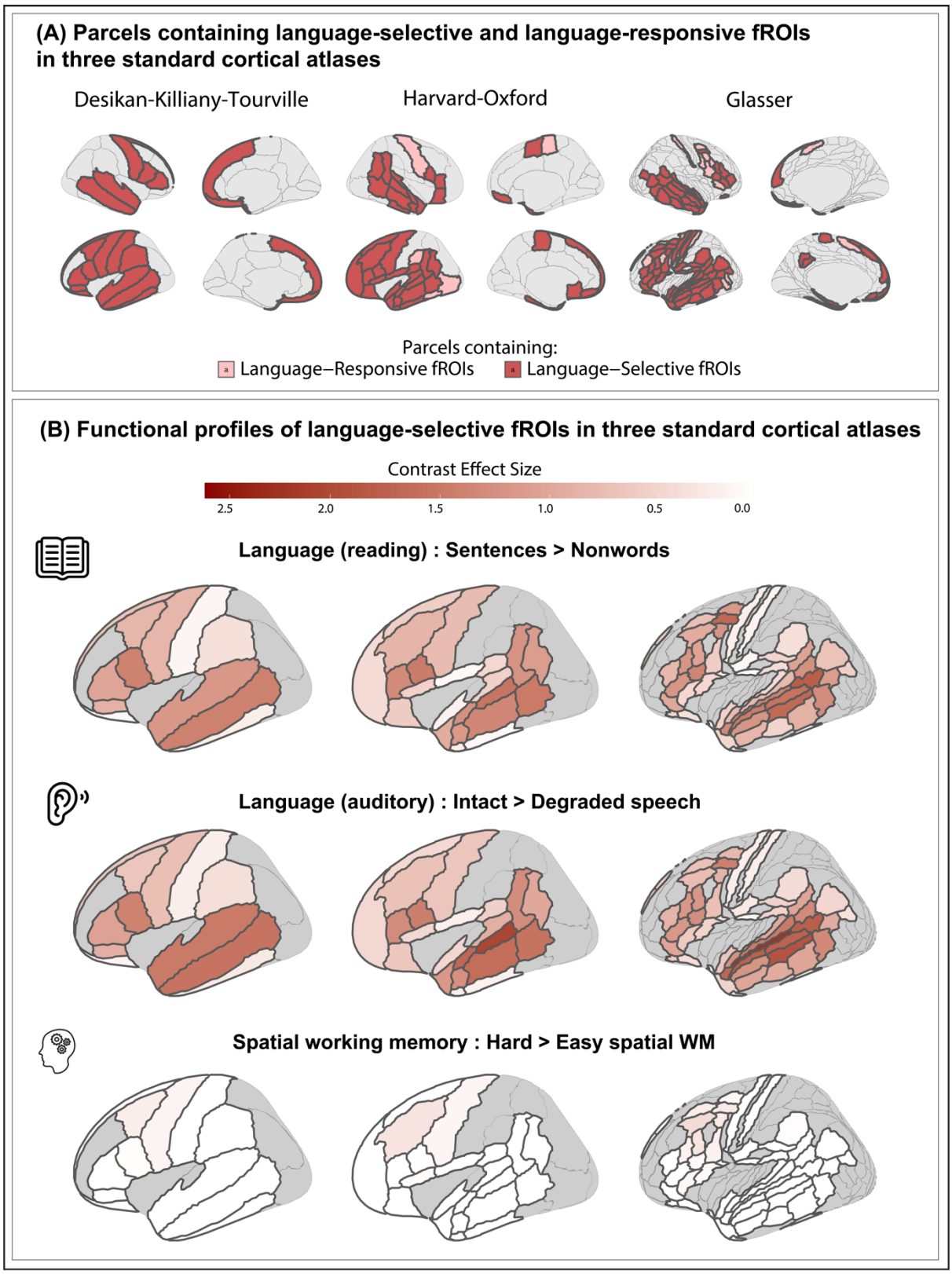

Figure 3. Language responsiveness and selectivity of the language fROIs within the parcels in three standard cortical atlases. Each column in both (A) and (B) panels corresponds to one of the three standard cortical parcellations (DKT: Klein & Tourville, 2012; HOC: Desikan et al., 2006; Glasser: Glasser et al., 2016). Panel (A) presents parcels that contain language-selective fROIs (marked in red) and language-responsive fROIs (marked in pink) in each atlas. Panel (B) visualizes—for the language fROIs that fall within the left lateral parcels—the effect sizes for the critical contrasts in the three tasks (corresponding to the three rows); top row:

reading-based language localizer (*Sentences* > *Nonwords*), middle row: auditory language localizer (*Intact* > *Degraded speech*), and bottom row: spatial working memory task (*Hard spatial WM* > *Easy spatial WM*). Note that in these visualizations, we color the entire parcels, but the language-responsiveness/selectivity and the effect sizes represent the properties of the individually-defined fROIs (i.e., top 10% of the most language-responsive voxels in each parcel, defined based on a portion of the data from the reading-based language localizer; Methods). (For a similar figure presenting all 4 brain views – left and right lateral and medial – see **SI Figure S5**).

Language-selective regions in the subcortical atlas

In the Harvard-Oxford Subcortical atlas, 4 of the 14 parcels that we examined (to the exclusion of the brain stem, ventricles, and white matter) contained language-selective fROIs: bilateral hippocampi and bilateral amygdalae (**Figure 5A**). One additional parcel (the left thalamus) contained a language-responsive, but non-selective fROI (**Figure 5B**; details of the statistical tests can be found in **Table 1** in the OSF repository at https://osf.io/7594t/).

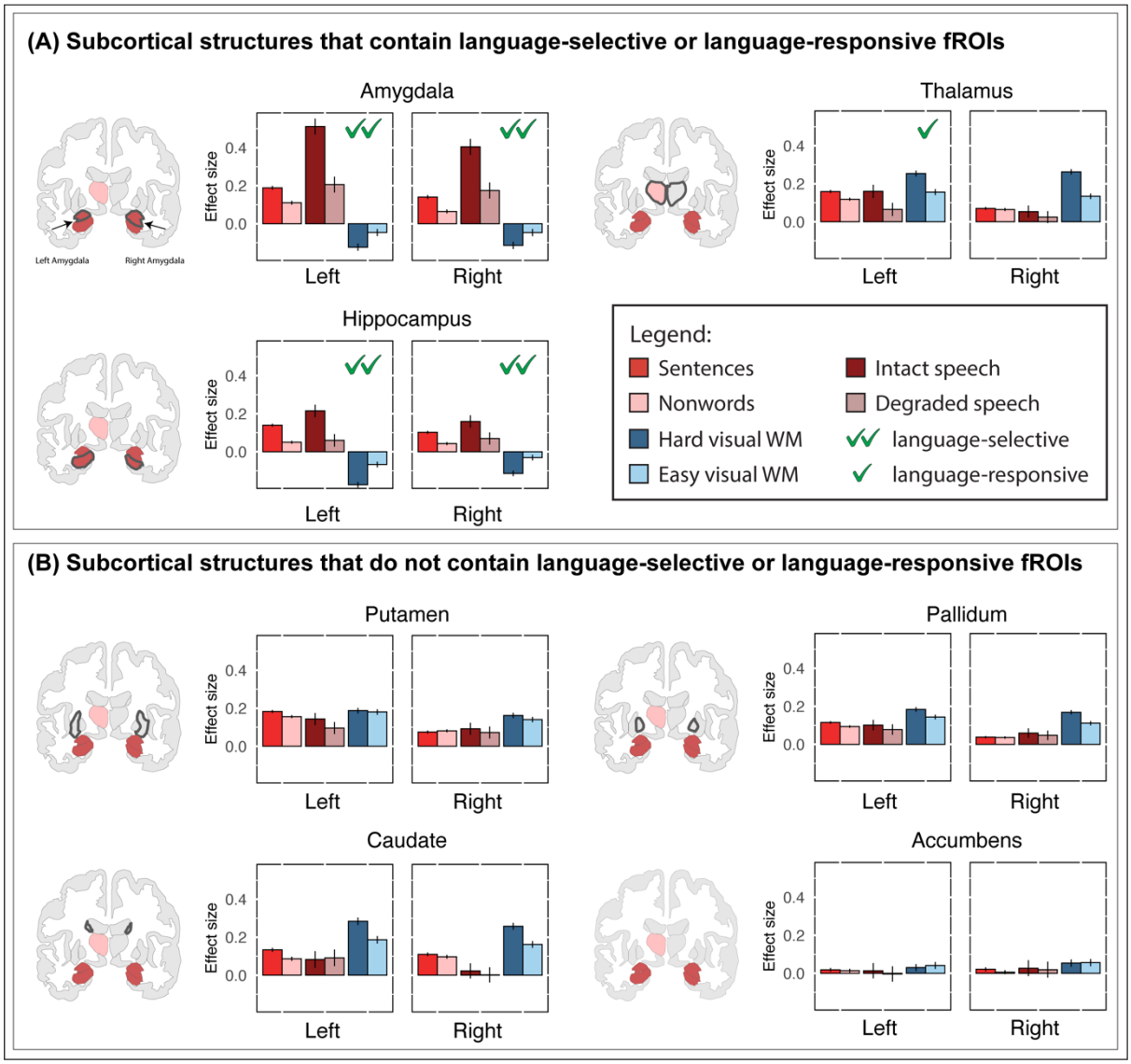

Figure 5. Language responsiveness and selectivity of the language fROIs within the parcels in the Harvard-Oxford Subcortical atlas. For each region (defined based on individual activation maps; Methods), we show responses to the reading-based and auditory language localizers (red bars; darker bars correspond to the critical conditions) and the non-linguistic spatial working memory task (blue bars; the darker bar corresponds to the harder condition). For the reading-based localizer, the responses were estimated using independent runs of the data from

the data used for fROI definition. Panel (A), marks the parcels that contain language-responsive fROIs with a green checkmark; the ones where the fROIs are additionally language-selective have two green checkmarks. Panel (B) shows the parcels that do not contain language-responsive fROIs.

Discussion

Many brain areas outside the left fronto-temporal network have been previously implicated in language processing. Here, we performed a systematic search for language-responsive areas across the brain. To do so, we a) used a paradigm that isolates language processing from perceptual, motor, and task-related cognitive demands (Fedorenko et al., 2010), b) included a large number of participants (n=772), c) examined language responses across modalities, and d) evaluated language selectivity relative to a demanding cognitive task. In addition to the core left hemisphere areas and their homotopes, we identified 17 areas (7 cortical, 5 cerebellar, 5 subcortical) that respond to auditory and written language, with 14 of these areas showing selectivity for language. These language-selective areas include bilateral temporal pole areas, a left ventral temporal area (putative BTLA; Lüders et al., 1986), three medial frontal areas, an area in the left precuneus, two areas in the right cerebellum and a homotopic left cerebellar area, and bilateral hippocampal and amygdala areas.

The contributions of non-canonical language areas to language and cognition.

Establishing that a brain area responds to language across modalities and not during a non-linguistic task ensures that its activity is not driven by perceptual or general cognitive demands. Still, the precise contributions of these language-responsive and language-selective areas remain to be discovered. Past studies may hold some clues, but relating our results to prior work is challenging: we cannot be certain that the areas we found here correspond to those identified in prior work, because macroanatomy is a poor guide to function (Frost & Goebel, 2012; Tahmasebi et al., 2012). Investigations of the core language areas have also faced this challenge (see Fedorenko & Kanwisher, 2009; Fedorenko et al., 2010 for discussion); however, adopting the functional localization approach has led to several robust and replicable findings about the language network, including its selectivity for language over diverse non-linguistic conditions (see Fedorenko et al., 2024 for a review). The newly identified language areas thus constitute new targets for similar systematic investigations, some already ongoing (Li et al., 2024; Lee et al., 2024; Casto et al., 2025).

Language-selective brain regions plausibly support language-specific computations related to word retrieval, syntactic structure building, or semantic composition. However, non-selective areas that reliably respond to language across modalities may still meaningfully contribute to language processing. We identified three such areas: two in the right cerebellum, and an area in the left thalamus. Higher spatial resolution approaches may eventually reveal that distinct neural sub-populations create the appearance of mixed selectivity. However, if the mixed selectivity turns out to be real, it may suggest that these regions play an integratory role, perhaps combining inputs from the core language areas and other areas. Indeed, both the cerebellum and the thalamus—where we find the non-language-selective responses—have been

hypothesized to serve as information integrators (Barbas et al., 2013; Theofanopoulou & Boeckx, 2016; Jobson et al., 2024).

Activation during a "language task" may not reflect linguistic processing.

Some past studies have reported neural activity during language tasks in areas that do not show language-responsiveness in our study. However, activation during a language task may not necessarily reflect linguistic processing. Specifically, many language paradigms tax both linguistic processing and task-related cognitive demands. A response in such paradigms could therefore reflect language but also other general cognitive processes (e.g., attention). For example, Thibault et al. (2021) have argued for an overlap between syntactic processing and tool use in the basal ganglia. However, both the syntactic and tool-use tasks require cognitive processes beyond syntactic and tool-use-related computations. We show that the language paradigms that are not confounded with task demands do not reliably engage any basal ganglia structures (**Figure 5B**; see also **Figure S2** in the **SI**), which suggests that the syntactic complexity manipulation in Thibault et al.'s study is engaging these areas due to the task demands and not by virtue of language-specific syntactic computations (see **Figure S3** in the **SI** for evidence that basal ganglia areas respond strongly to task demands).

Similarly, Seydell-Greenwald et al. (2023) report responses to language tasks (auditorily-presented) in the primary visual cortex (V1). However, their language contrasts are confounded with attentional demands: one compares listening to sentences and answering questions about them vs. listening to reversed speech and responding to a beep (see Ozernov-Palchik, O'Brien et al., 2024 for a discussion of attention/difficulty confounds in this paradigm), and the other involves listening to words and pressing a button in response to catch trials, thus requiring attention to the task beyond the lexical processing demands. Attentional modulation of V1 is well-established (Somers et al., 1999), so responses in V1 during language tasks that require attention plausibly reflect attention-related engagement. In our study, we see some response in occipital areas to the reading-based contrast, but it does not generalize to the auditory modality, which rules out the possibility that V1 of sighted individuals implements linguistic computations (cf. evidence of V1 supporting language processing in congenitally blind individuals; Bedny et al., 2011; Lane et al., 2015; Pant et al., 2020).

To summarize, to argue that a brain area supports linguistic computations, one needs to ensure that the language task is not confounded by difficulty or attentional demands. Previous work has established that the core language areas are relatively insensitive to task demands, showing similarly strong responses during passive comprehension and paradigms that include tasks (Fedorenko et al., 2010; Diachek, Blank, Siegelman, et al., 2020), and here, we extend these findings to several non-canonical language areas but question some past findings of language responses that can be reinterpreted in alternative ways.

A small and well-defined subset of the brain implements language processing.

Despite ample evidence for functional specialization in both humans (e.g., Kanwisher, 2010) and non-human animals (e.g., Tsao et al., 2006), some continue to argue against the idea of stable structure in the brain, emphasizing the distributed, dynamic, and interactive nature of

cognitive processes (e.g., Pessoa, 2022; Forkel & Hagoort, 2024; Drijvers et al., 2025). Deep engagement with this debate is beyond the scope of this article, but we see an opportunity to clarify two points. First, the fact that many areas—sometimes in distant parts of the brain—are engaged by language comprehension does not imply that the "entire brain" supports this process. Although the extended language network spans almost every major component of the brain, within each component (e.g., the left inferior frontal cortex or the cerebellum), language regions occupy a tiny fraction of brain tissue. As discussed in the Results, the entire language network constitutes <1.5% of the brain volume and is about the size of a large strawberry. Second, the fact that the language network needs to interact with other areas does not undermine its functional distinctiveness from those areas and its special role in language processing. As long as different components within the language network are more strongly connected to one another than to other networks—for which ample evidence exists (Blank et al., 2014; Braga et al., 2020; Shain et al., 2025)—those networks can be treated as distinct objects of study (Simon, 1962).

Parcels derived from functional data have an advantage over anatomical parcels for constraining individual fROIs.

One advantage of functional localization is that it ensures analysis of the same region across participants, but deciding which bit of activation in one brain corresponds to which bit in another brain requires some anatomical constraints. Fedorenko et al. (2010; Julian et al., 2012) developed the group-constrained-subject-specific (GSS) approach, which derives these constraints (parcels) from a group-level representation of the activity for a particular contrast. In this way, the parcels respect the topography of the relevant area/network.

Here, in addition to the GSS approach, we explored the possibility of using anatomical parcels from standard atlases to constrain individual fROIs. Such atlases may work well for subcortical structures with clearly defined boundaries (Desikan et al., 2006), but they are not optimal for cortical areas. Some atlases divide the cortex coarsely into a small number of large regions. More modern, multimodal atlases yield a finer-scale brain parcellation (Glasser et al., 2016; Schaefer et al., 2018). However, examining individual activation maps (or maps derived from voxel-level clustering during naturalistic cognition; e.g., (Braga et al., 2020; Du et al., 2020, 2025; Shain et al., 2025) against standardized brain parcellations reveals that the boundaries of atlas areas often do not align with the individual topographies: a contiguous functional region may get broken up by a boundary, or—especially in fine-scale parcellations—the same functional region may get assigned to different atlas areas across individuals because of inter-individual topographic variability (see **SI Figure S6** for examples). For studies focusing on a particular functional network, we therefore recommend functional parcels over anatomical/multimodal atlases. Critically, however, whichever approach is chosen, the regions of analysis should be defined functionally within individuals (using localizers or functional-connectivity-based parcellations; Braga et al., 2020; Du et al., 2020, 2025; Shain et al., 2025) to avoid conflating nearby networks at the group level (**Figure 3B**; see also **SI Figure S2** and **S3** for evidence that most of the language parcels also include domain-general areas).

In conclusion, we have comprehensively searched for language-selective areas across the brain and identified several new components of the extended language network. This work lays the groundwork for future investigations of these new components, including their similarities to and differences from the core language areas.

Table 2. List of parcels that contain language-responsive and language-selective fROIs in the three standard cortical atlases: the DKT, Harvard-Oxford Cortical, and Glasser atlases. In the Glasser atlas, parcels marked with a degree sign (º) lie at the intersection of two anatomical lobes and parcels marked with a cross lie at the intersection of three anatomical lobes and are thus listed in more than one lobe.

Parcels in the DKT atlas that contain language-selective* fROIs

Lobe	Left hemisphere	Right hemisphere
Frontal	Caudal Middle Frontal, Medial Orbitofrontal, Pars Opercularis, Pars Orbitalis, Pars Triangularis, Precentral, Superior Frontal, Lateral Orbitofrontal	Medial Orbitofrontal, Pars Opercularis, Pars Triangularis, Precentral, Superior Frontal
Parietal	Supramarginal, Postcentral	
Temporal	Inferior Temporal, Middle Temporal, Superior Temporal	Middle Temporal, Superior Temporal

Parcels in the Harvard-Oxford Cortical atlas that contain language-selective fROIs

Lobe	Left hemisphere	Right hemisphere
Frontal	Frontal Pole, Sup. Frontal Gyrus, Mid. Frontal Gyrus, Inf. Frontal Gyrus Pars Triangularis, Inf. Frontal Gyrus Pars Opercularis, Precentral Gyrus, Frontal Medial Cortex, Juxtapositional Lobule Cortex, Frontal Orbital Cortex, Frontal Operculum Cortex	Inf. Frontal Gyrus Pars Triangularis, Inf. Frontal Gyrus Pars Opercularis, Frontal Medial Cortex, Frontal Orbital Cortex, Juxtapositional Lobule Cortex
Parietal	Supramarginal Gyrus Post., Angular Gyrus, Central Opercular Cortex, Parietal Operculum Cortex	Supramarginal Gyrus Post., Angular Gyrus
Temporal	Temporal Pole, Sup. Temporal Gyrus Ant., Sup. Temporal Gyrus Post., Mid. Temporal Gyrus Ant., Mid. Temporal Gyrus Post., Mid. Temporal Gyrus Temporooccipital, Inf. Temporal Gyrus Ant., Inf. Temporal Gyrus Post., Temporal Fusiform Cortex Ant., Temporal Fusiform Cortex Post., Planum Polare, Planum Temporale	Temporal Pole, Sup. Temporal Gyrus Ant., Sup. Temporal Gyrus Post., Mid. Temporal Gyrus Ant., Mid. Temporal Gyrus Post., Mid. Temporal Gyrus Temporooccipital, Inf. Temporal Gyrus Ant., Planum Temporale, Temporal Fusiform Cortex Ant.
Occipital		Lat. Occipital Cortex Inf.
	Additional parcels that contain language-responsive (but not language-selective) fROIs	
Frontal		Precentral Gyrus
Parietal		Supramarginal Gyrus Ant.
Temporal	Inf. Temporal Gyrus Temporooccipital	
Occipital		Lat. Occipital Cortex Inf.

Parcels in the Glasser atlas that contain language-selective fROIs

Lobe	Left hemisphere	Right hemisphere
Frontal	FEF, PEF, 4, 55B, SFL, 8C, 8BM, 10R, 47M, 9M, 9P, 44, 45, 47L, 6R, 8AV,	55B, SFL, 47M, 9M, 8BL, 44, 45, IFJA, IFSP, IFSA, 10V, OFC

	8BL, IFJA, IFSP, IFSA, 9A, 10V, 10d, 47S, FOP5, S32°, FOP4°, OP4°, OP2-3°, FOP1	
Parietal	3b, PFCM, PF, OP4°, 31PD°, PGI†, PSL°, OP2-3°	
Occipital	PGI†, PHT°, TPOJ3	PHT°, TOPJ3
Temporal	FOP4°, PEEC°, PGI†, PSL°, STV, RI, TA2, STGA, PBELT, A5, STSDA, STSDP, STSVP, TGD, TE1A, TE1P, TF, TE2P, TPOJ1, TPOJ2, TGV, A4, STSVA, TE1M, PI, PIR°, PHT°, OP2-3°	STV, TA2, STGA, A5, STSDA, STSDP, STSVP, TGD, TE1A, TE1P, TPOJ1, TPOJ2, TGV, A4, STSVA, TE1M, PHT°
Limbic**	S32°, 31PV, PEEC°, 31PD°, PIR°, H, pOFC	
	Additional parcels that contain language-responsive (but not language-selective) fROIs	
Frontal	1, SCEF, 6D, 6V, IFJP, P9-46V, I6-8, PHA3	1, 6r, FOP5
Temporal		TF
Occipital	MST, FST	

* All DKT language-responsive regions are also language-selective.

** Lobe segmentation in the Glasser parcellation follows PALS_B12 atlas (Van Essen, 2005; https://surfer.nmr.mgh.harvard.edu/fswiki/PALS_B12) template (using FreeSurfer);

° denotes regions straddling two lobes;

† denotes regions straddling three lobes.

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