

Functional specificity for high-level linguistic processing in the human brain

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Neuroscientists have debated for centuries whether some regions of the human brain are selectively engaged in specific high-level mental functions or whether, instead, cognition is implemented in multifunctional brain regions. For the critical case of language, conflicting answers arise from the neuropsychological literature, which features striking dissociations between deficits in linguistic and nonlinguistic abilities, vs. the neuroimaging literature, which has argued for overlap between activations for linguistic and nonlinguistic processes, including arithmetic, domain general abilities like cognitive control, and music. Here, we use functional MRI to define classic language regions functionally in each subject individually and then examine the response of these regions to the nonlinguistic functions most commonly argued to engage these regions: arithmetic, working memory, cognitive control, and music. We find little or no response in language regions to these nonlinguistic functions. These data support a clear distinction between language and other cognitive processes, resolving the prior conflict between the neuropsychological and neuroimaging literatures.

functional specialization | modularity | functional MRI | sentence understanding

Language is our signature cognitive skill, uniquely and universally human. Does language rely on dedicated cognitive and neural machinery specialized for language only, or is it supported by the same circuits that enable us to perform arithmetic, hold information in working memory, or appreciate music?

The neuropsychological literature features striking dissociations between deficits in linguistic and nonlinguistic abilities (1–6). In contrast, prior neuroimaging work has suggested that brain regions that support language—especially regions on the lateral surface of the left frontal lobe—also support nonlinguistic functions (7–23). However, the neuroimaging claims are based largely on observations of activation for a nonlanguage task in or near a general brain region previously implicated in language (e.g., Broca's area), without a direct demonstration of overlap of linguistic and nonlinguistic activations in the same subjects. Such findings do not suffice to demonstrate common brain regions for linguistic and nonlinguistic functions in the brain. Even when two tasks are compared in the same group of subjects, standard functional MRI group analysis methods can be deceptive: two different mental functions that activate neighboring but non-overlapping cortical regions in every subject individually can produce overlapping activations in a group analysis, because the precise locations of these regions vary across subjects (24–26), smearing the group activations. Definitively addressing the question of neural overlap between linguistic and nonlinguistic functions requires examining overlap within individual subjects (27, 28), a data analysis strategy that has almost never been applied in neuroimaging investigations of high-level linguistic processing.

Here, we used functional MRI to test the functional specificity of brain regions engaged in language processing by identifying brain regions that are sensitive to high-level linguistic processing in each subject individually and then asking whether these same regions are also engaged when the subject performs nonlinguistic

tasks. Specifically, we examined the response of high-level language regions to seven nonlinguistic tasks that tap the cognitive functions most commonly argued to recruit the language network: exact arithmetic (experiment 1), working memory (WM; experiments 2 and 3), cognitive control (experiments 4–6), and music (experiment 7).

For the language localizer task, participants read sentences and strings of pronounceable nonwords and decided whether a subsequent probe (a word or nonword, respectively) appeared in the preceding stimulus (Fig. 1). The sentences > nonwords contrast targets brain regions engaged in high-level linguistic processing (sentence understanding), including lexical and combinatorial processes but excluding phonological and other lower-level processes.^{*} This localizer was previously shown (29) to robustly and reliably identify each of the key brain regions previously implicated in high-level linguistic processing (30, 31) (Fig. 2 and Fig. S1) in at least 80% of subjects individually and to be robust to changes in stimulus modality (visual/auditory) (see also ref. 32), specific stimuli, and task (passive reading vs. reading with a probe task, which is used here). Furthermore, unlike the language contrasts used in some prior studies (17, 21), this contrast does not confound linguistic processing and general cognitive effort, because the memory probe task is more difficult in the control (nonwords) condition.

For all nonlinguistic functions, we chose tasks and contrasts commonly used in previous published studies (Fig. 1 and *Materials and Methods*). Experiments 1–6 each contrasted a condition that was more demanding of the nonlinguistic mental process in question and a closely matched control condition that was less demanding of that mental process (see Table S3 for behavioral results). Engagement of a given region in a given mental process would be shown by a higher response in the difficult condition than the easy condition. Given previous findings (33–35), we expected these tasks to activate frontal and parietal structures bilaterally. Experiment 7 contrasted listening to intact vs. scrambled music. Engagement of a given region in music would be shown by a higher response to intact than scrambled music. Given previous findings (3, 20, 36), we expected this contrast to activate frontal and temporal brain regions. The critical question is whether the activations for nonlinguistic task contrasts will overlap with activations for the language task.

Author contributions: E.F. and N.K. designed research; E.F. and M.K.B. performed research; E.F. analyzed data; and E.F. and N.K. wrote the paper.

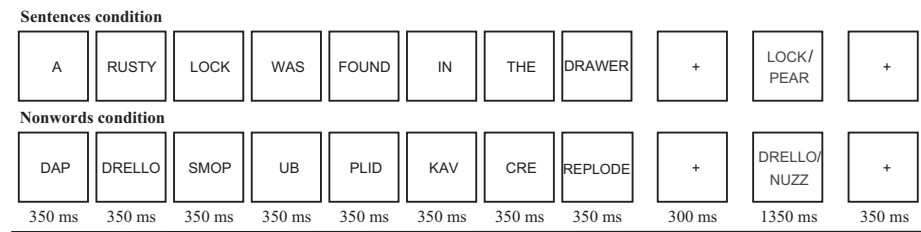
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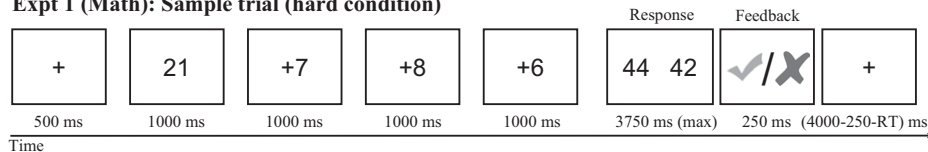
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^{*}Of course, the question of the relationship between linguistic and nonlinguistic processes extends to other aspects of language (e.g., sound-level processes), which we are not targeting with the current language localizer task. However, most claims about the overlap between linguistic and nonlinguistic processes have concerned (i) syntactic processing, which is included in our functional contrast, and (ii) brain regions, which are robustly activated by our localizer (e.g., Broca's area).

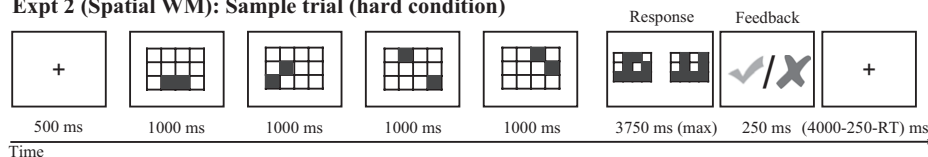
Language localizer: Sample trials



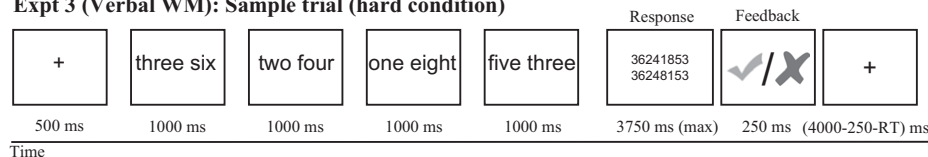
Expt 1 (Math): Sample trial (hard condition)



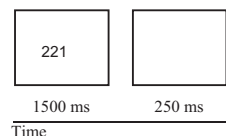
Expt 2 (Spatial WM): Sample trial (hard condition)



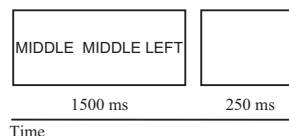
Expt 3 (Verbal WM): Sample trial (hard condition)



Expt 4 (MSIT): Sample trial (hard condition)



Expt 5 (vMSIT): Sample trial (hard condition)



Expt 6 (Stroop): Sample trial (hard condition)

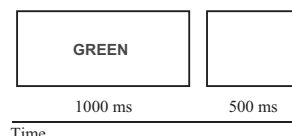


Fig. 1. Sample trials for the localizer task and nonlinguistic tasks in experiments 1–6. In the math task, participants added smaller vs. larger addends. In the spatial/verbal WM tasks, participants remembered four vs. eight locations/digit names. In the multisource interference task (MSIT), participants saw triplets of digits and had to press a button corresponding to the identity of the nonrepeated digit. The hard condition involves two kinds of conflict: between the spatial position of the target response and the position of the response button and between the target response and the distracter elements. The verbal MSIT (vMSIT) task was a slight variant of the MSIT, where words were used instead of digits. In the Stroop task, participants overtly named the font color vs. noncolor adjectives. In the music task, participants listened to unfamiliar Western tonal pieces vs. the scrambled versions of these pieces (*Materials and Methods* has details).

Results

Language Activations. As expected, reading sentences elicited a reliably stronger response than reading nonwords in each region of interest (ROI) (*Materials and Methods*, Fig. 2, black and gray bars, and Fig. S1, black and gray bars) (here and throughout the study, responses were estimated using data from left-out runs not used for defining the ROIs).

Overlap Between Language and Nonlinguistic Tasks: ROI Analyses.

Fig. 2 and Tables S1 and S2 show our key results: the response in each of the left hemisphere language-sensitive ROIs during each of the seven nonlinguistic tasks (Fig. S1 has the responses of right hemisphere and cerebellar regions). Although each nonlinguistic task produced robust activations at the individual subject level in nearby brain regions (Fig. 3), they had little effect in the language ROIs. The music contrast did produce some response in several language ROIs (*SI Text*), suggesting possibly overlapping circuits; however, these effects were weak overall, and none survived cor-

rection for multiple comparisons. One frontal language ROI left middle frontal gyrus (LMFG) showed a significant response to verbal working memory after correcting for the number of ROIs; this region is, thus, not specialized for sentence understanding. However, no other ROIs showed reliable responses to any of the nonlinguistic tasks, indicating a striking degree of functional specificity for language processing.

In several ROIs, some of the nonlinguistic tasks resulted in deactivation relative to the fixation baseline. These patterns simply indicate that the region in question was more active during rest (when participants are plausibly engaged in daydreaming, presumably sometimes including verbal thinking) than during the task in question.

Overlap Between Language and Nonlinguistic Tasks: Whole-Brain Analyses.

ROI-based analyses afford great statistical power and reduce the blurring of functional activations inevitable in group analyses. However, ROI analyses can obscure functional heterogeneity within an ROI or miss important overlapping regions

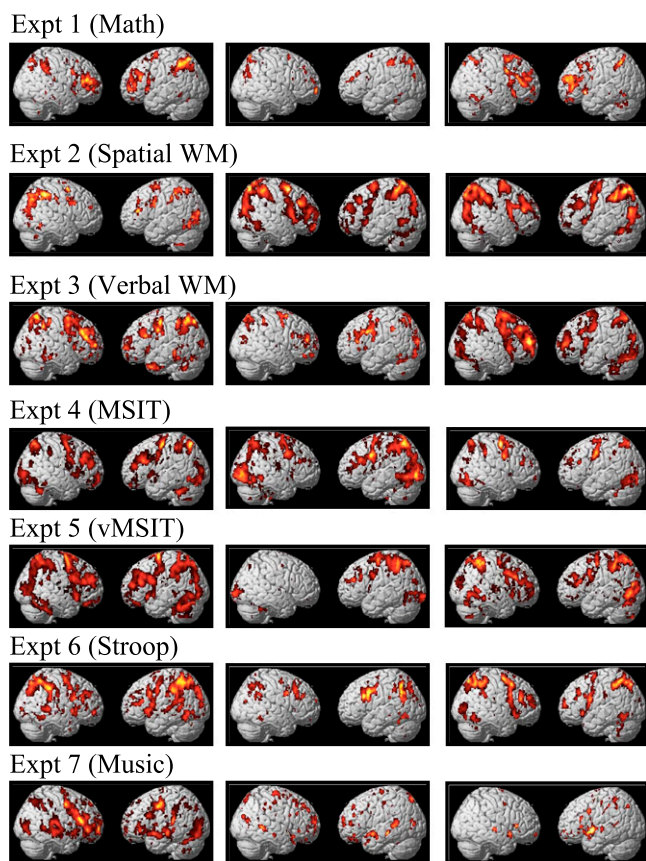


Fig. 3. Sample individual activation maps (thresholded at $P < 0.001$, uncorrected) for the nonlinguistic tasks showing three representative subjects from each experiment. For experiments 1–6, the contrast is hard > easy; for experiment 7, the contrast is intact > scrambled.

Discussion

The current results show that most of the key cortical regions engaged in high-level linguistic processing are not engaged by mental arithmetic, general working memory, cognitive control, or musical processing, indicating a high degree of functional specificity in the brain regions that support language. The one exception is a brain region located in the left middle frontal gyrus that seems to support both high-level linguistic processing and verbal working memory.

The ROI corresponding roughly to Broca's area (LIFG) (Fig. 2) has been a major target of prior research, and we chose nonlinguistic tasks that could test the main hypotheses that have been proposed about the possible nonlinguistic function(s) of this region. Our data are difficult to reconcile with the widely favored hypothesis that this region is engaged in domain general cognitive control (8, 17); although we do see a weak response to the Stroop task in this region, we find no hint of activation for either of the other two cognitive control tasks [the MSIT task (39) and its variant, verbal MSIT (vMSIT)]. Furthermore, although this region does respond more strongly to intact than scrambled musical stimuli (consistent with some previous claims) (21), the response to intact music is barely above the fixation baseline (and lower than the response to the language localizer control task), making it difficult to argue that this region supports general structural processing of complex stimuli that unfold over time (9, 20, 21).

The nature of the computations in the posterior part of the LIFG language ROI that seems to support not only sentence understanding but also verbal WM and the mental processes re-

quired for the Stroop task (Fig. 4) remains an open question. This region—like the language ROI encompassing it (LIFG ROI)—is unlikely to support domain general cognitive control, because no overlap regions emerged in posterior LIFG between language and the other two cognitive control tasks (MSIT and vMSIT), consistent with the lack of a response to these tasks in the LIFG language ROI. Moreover, the fact that this region responds to the verbal WM task, which is not traditionally considered to tax cognitive control processes, suggests that this region may instead support demanding cognitive tasks when they involve storing or manipulating verbal representations. It is also possible, however, that, at higher spatial resolution, we would discover that this apparent overlap is artifactual, merely reflecting the proximity of the language-sensitive cortical regions to those regions that support demanding cognitive tasks (ref. 40 has a similar demonstration in the ventral visual cortex).

More generally, the current data pose a challenge for hypotheses that brain regions that support high-level aspects of language also (i) represent and manipulate exact quantity information (7, 22, 23), (ii) contribute to language processing through domain general working memory or cognitive control mechanisms (8, 17), or (iii) process structured sequences unfolding over time regardless of their content (9, 16, 20).

Note that the brain regions investigated here are surely not the only ones engaged in or necessary for language processing. Understanding language requires perceiving linguistic input either auditorily (hence, requiring auditory cortex) or visually (hence, requiring visual cortex), and producing language requires parts of motor cortex. In addition, frontal and parietal brain regions engaged in a very domain general fashion in many demanding cognitive tasks (33–35) may be necessary for many aspects of linguistic function. Thus, language processing probably requires both the very specialized regions studied here and more domain general regions.

Of course, discovering that a brain region is selectively engaged in linguistic processing is just a first step. Ultimately, we want to know the precise computations conducted and the representations extracted in each of these regions as well as how different components of the language system work together to enable us to produce and understand language. Existing frameworks (41–44) provide an important foundation, but future work should strive to develop computationally precise and testable hypotheses for each of the core language regions.

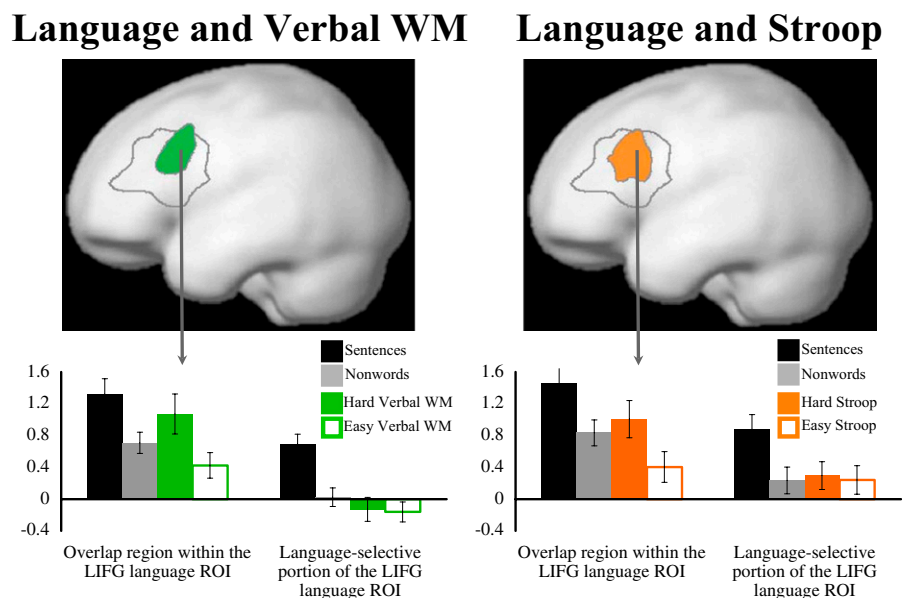
To conclude, discoveries of linguistic specificity provide answers to the longstanding question of whether high-level cognitive functions are supported by dedicated neural machinery (45) and provide important clues into the mental operations supported by these regions. Future work will (i) test the engagement of regions that support high-level linguistic processing in yet other nonlinguistic processes (e.g., amodal conceptual processing, action representation, or hierarchical sequence processing) as well as examine other language regions that support phonological and discourse-level processes, (ii) identify the precise linguistic computations conducted in each of these regions, and (iii) characterize the interactions between these regions and other parts of the brain that enable uniquely human cognition.

Materials and Methods

Participants. Forty-eight right-handed participants (31 females) from Massachusetts Institute of Technology (MIT) and the surrounding community were paid for their participation. All were native speakers of English between the ages of 18 and 40 y, had normal or corrected to normal vision, and were naive as to the purposes of the study. All participants gave informed consent in accordance with the requirements of the Internal Review Board at MIT.

Design. Each participant was run on the language localizer task (which included the sentences condition and the pronounceable nonwords condition) and one or more nonlinguistic tasks. Each nonlinguistic task included two conditions (hard and easy for tasks in experiments 1–6 and intact music and scrambled music in experiment 7) (Fig. 1).

Fig. 4. Key results from the whole-brain overlap analysis with very liberally thresholded ($P < 0.05$, uncorrected) individual activation maps (*Materials and Methods* has details). Similar overlap regions—in the posterior part of the LIFG language ROI (whose outline is shown in gray above)—emerged in the analyses of language and verbal WM (green; present in 85% of the subjects with an average size of 76 voxels) and language and Stroop (orange; present in 71% of the subjects with an average size of 95 voxels). The left set of bars in each panel shows the responses of these overlap regions to the four conditions (estimated in left-out runs). The right set of bars in each panel shows the results of a complementary analysis where we examined voxels within the LIFG language ROI that respond to the language localizer contrast (at $P < 0.001$, uncorrected) but not to the non-linguistic task contrast (at $P < 0.1$). Responses to the four conditions were again estimated using left-out runs. In each dataset, a substantial proportion of voxels (127/355 voxels, on average, in the language-Verbal Working Memory dataset and 163/410 voxels in the language-Stroop dataset) showed replicable selectivity for the language task, suggesting that a portion of the LIFG language ROI is selectively engaged in sentence understanding.



Language localizer. Participants read sentences and pronounceable nonword lists and presented one word/nonword at a time. After each stimulus, a memory probe appeared, and participants decided whether the probe word/nonword appeared in the preceding stimulus.

The localizer is available to download at http://web.mit.edu/evelina9/www/funcloc/funcloc_localizers.html.

Nonlinguistic tasks. In experiment 1 (math), participants ($n = 11$) saw a number (11–30) and added three addends to it (of sizes two to four or six to eight in the easy and hard conditions, respectively).[†] After each trial, participants had to choose the correct sum in a two-choice forced choice question (the incorrect sum deviated by one to two). Participants were told whether they answered correctly. Each run (consisting of 10 34-s-long experimental and 6 16-s-long fixation blocks) lasted 436 s. Each participant did two to three runs. (The same timing was used in experiments 2 and 3.) In experiment 2 (spatial WM), participants ($n = 12$) saw a 3×4 grid and kept track of four or eight locations in the easy and hard conditions, respectively. After each trial, participants had to choose the grid with the correct locations in a two-choice question (the incorrect grid contained one to two wrong locations). In experiment 3 (verbal WM), participants ($n = 13$) kept track of four- or eight-digit names in the easy and hard conditions, respectively. Digits were presented as words (e.g., three) to prevent chunking (e.g., to prevent 3 5 from being encoded as thirty-five). After each trial, participants had to choose the correct digit sequence in a two-choice question (in the incorrect sequence, the identity of one or two digits, with respect to serial position, was incorrect). In experiment 4 (MSIT), participants ($n = 15$) saw triplets of digits (possible digits included zero, one, two, and three) and pressed a button (one, two or three; laid out horizontally on a button box) corresponding to the identity of the nonrepeated digit. In the easy condition, the position of the nonrepeated digit corresponded to the position of the response button, and the other digits were not possible responses (e.g., 100); in the hard condition, the position of the nonrepeated digit did not correspond to the position of the button, and the other digits were possible responses (e.g., 212). The timing was as described in ref. 39. Each participant did three to five runs. Experiment 5 (VMSIT, $n = 12$) was identical to experiment 4, except that digits (zero, one, two, and three) were replaced with words (none, left, middle, and right) to see whether more verbal representations would lead to greater overlap with the language activations. In experiment 6 (Stroop), participants ($n = 14$) saw a word and overtly named the color of the word's font. In the easy condition, the words were noncolor adjectives (huge, close, and guilty) matched to the color adjectives in length and lexical frequency; in the hard condition, the words were color adjectives (blue, green, and

yellow), and in one-half of the trials in each block, the font color did not match the color that the word indicated. Experimental and fixation blocks lasted 18 s each. Each run (16 experimental and 5 fixation blocks) lasted 378 s. Each participant did two to three runs. In experiment 7 (music), participants ($n = 12$) heard 64 unfamiliar musical pieces (pop/rock music from the 1950s and 1960s) over the scanner-safe headphones. To scramble musical structure, we altered the pitch and timing of musical notes in Musical Instrument Digital Interface representations of the pieces. For each piece, a random number of semitones between -3 and 3 was added to the pitch of each note to make the pitch distribution approximately uniform. The resulting pitch values were randomly reassigned to the notes of the piece to remove the contour structure. To remove the rhythmic structure, the note onsets were jittered by up to 1 beat duration (uniformly distributed), and the note durations were randomly reassigned. The resulting piece had component sounds similar to the intact music but lacked musical structure. (The experiment included two additional conditions, with only the pitch contour or rhythm scrambled, but we focus on the intact and scrambled conditions here.) For eight participants, the task was passive listening (to help participants stay awake, we asked them to press a button after each piece); the last four participants were asked the question, "How much do you like this piece?" after each stimulus. Because the activation patterns were similar across the two tasks, we collapsed the data from these two groups of participants for the current analyses. Experimental and fixation blocks lasted 24 and 16 s, respectively. Each run (16 experimental and 5 fixation blocks) lasted 464 s. Each participant did four to five runs.

Data Acquisition. Structural and functional data were collected on the whole-body 3-Tesla Siemens Trio scanner at the Athinoula A. Martinos Imaging Center at the McGovern Institute for Brain Research at MIT. T1-weighted structural images were collected in 128 axial slices with 1.33-mm isotropic voxels [repetition time (TR) = 2,000 ms and echo time (TE) = 3.39 ms]. Functional, blood oxygenation level-dependent data were acquired in $3.1 \times 3.1 \times 4$ -mm voxels (TR = 2,000 ms and TE = 30 ms) in 32 near-axial slices. The first 4 s of each run were excluded to allow for steady state magnetization. The scanning session included several functional runs. The order of conditions was counterbalanced; each condition was equally likely to appear in the earlier vs. later parts of each run and was as likely to follow every other condition as it was to precede it.

Statistical Analysis. MRI data were analyzed using SPM5 (<http://www.fil.ion.ucl.ac.uk/spm>) and custom matlab scripts (available from <http://web.mit.edu/evelina9/www/funcloc.html>). Each subject's data were motion-corrected and then, they were normalized onto a common brain space (the Montreal Neurological Institute template) and resampled into 2-mm isotropic voxels. Data were smoothed using a 4-mm Gaussian filter and high pass-filtered (at 200 s). Language-sensitive ROIs were defined by intersecting (\cap) the parcels generated

[†]Overlapping sets of subjects were run on different nonlinguistic tasks; hence, the total number of participants ($n = 48$) is less than the sum of all of the numbers of participants across the seven experiments.

based on a group-level representation of the localizer data in a separate experiment (the parcels' outlines are shown in blue in Fig. 2 and Fig. S1) and (ii) individual subjects' localizer maps thresholded at $P < 0.001$, uncorrected (29).

For the ROI-based analyses, in every subject, the responses to each condition were averaged across the voxels within each region. The responses were then averaged across subjects for each region. The responses to the sentences and nonwords conditions were estimated using cross-validation across the functional runs, and therefore, the data used to estimate the effects were always independent of the data used for ROI definition (46). (For example, in a sample scenario of two functional runs, run 1 would be used to define the ROI, and run 2 would be used to estimate the effects. Then, run 2 would be used to define the ROI, and run 1 would be used to estimate the effects. Finally, the estimates would be averaged across the two runs.)

For the whole-brain overlap analyses, we overlaid activation maps (thresholded at $P < 0.001$, uncorrected, or $P < 0.05$, uncorrected, for the liberal thresholding version of the analyses) for (i) the language localizer and (ii) the relevant nonlinguistic task (e.g., Stroop hard > Stroop easy or intact music > scrambled music) in each subject. We then examined the overlap voxels (i.e., voxels responding to both the language localizer and the nonlinguistic task) across subjects to see if any meaningful overlap regions emerge (we used the group-constrained subject-specific method to perform this search for spatially systematic regions) (29). Meaningful overlap regions were defined as regions

that (i) are present in 80% or more of the individual subjects (i.e., have at least one voxel satisfying the predefined criteria, such as a significant response to both the language localizer and the nonlinguistic task, within the borders of the resulting region) and (ii) show replicable effects with cross-validation in a left-out subset of the data.

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