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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.

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 nonoverlapping 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 Table 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.

The authors declare no conflict of interest.

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2Of 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).
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 correction 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. 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).
outside the borders of the ROI. We, therefore, conducted additional analysis that did not use our language ROIs but instead, searched the whole brain for any regional consistency across subjects in the overlap between language activations and each of the nonlinguistic tasks (Materials and Methods).

At the threshold used for the ROI analyses, no spatially systematic regions were detected in which language activations overlapped with any of the seven nonlinguistic tasks, confirming the overall picture of language specificity found in the ROI analyses. [This threshold is not too stringent to discover true overlap when it exists; at the same threshold, we discovered robust overlap regions in the frontal and parietal lobes between Stroop and the multisource interference task (MSIT) cognitive control task in a subset of the subjects run on both tasks.]

To maximize our chances of discovering activation overlap, we performed the same analysis again but now with very liberally thresholded individual maps. This analysis discovered three overlap regions. Two of these regions were fully consistent with the results of the ROI analyses: one region was located within the LMFG language ROI and responded to both language and verbal WM, and another region was within the LMidPostTemp language ROI and responded to language and music (SI Text and Fig. S2). The third region, present in 85% of the subjects, emerged in the posterior part of our left inferior frontal gyrus (LIFG) language ROI and responded to both language and verbal WM (a similar region emerged in the analysis of the overlap of language and Stroop activations, although it was present in only 71% of the subjects) (Fig. 4). The existence of this overlap region in posterior LIFG is consistent with the weak trends that we found in the LIFG language ROI for verbal WM and Stroop. Furthermore, it is consistent with evidence for fine-grained cytoarchitectonic subdivisions within Broca’s area (37, 38). Nevertheless, a complementary analysis shows that a portion of the LIFG language ROI is selective for high-level linguistic processing and not engaged in either verbal WM or Stroop (Fig. 4).

![Fig. 2. Responses of the left hemisphere language ROIs to the language task (black, sentences; gray, nonwords; estimated using data from left-out runs) and the nonlinguistic tasks (shown in different colors, with the solid bar showing the response to the hard (experiments 1–6)/intact music (experiment 7) condition and the nonfilled bar showing the response to the easy/scrambled music condition). Individual subjects’ ROIs were defined by intersecting the functional parcels (shown in blue contours) with each subject’s thresholded (P < 0.001, uncorrected) activation map for the language localizer. The functional parcels were generated a priori based on a group-level representation of localizer activations in an independent set of subjects (29). Asterisks indicate significant effects (Bonferroni-corrected for the number of regions). The sentences > nonwords effect was highly significant (P < 0.0001) in each functional ROI. The only significant effect for the nonlinguistic tasks was the hard > easy verbal WM effect in the LMFG functional ROI (P < 0.005). Tables S1 and S2 have detailed statistics.](www.pnas.org/cgi/doi/10.1073/pnas.1112937108)
Expt 1 (Math)
Expt 2 (Spatial WM)
Expt 3 (Verbal WM)
Expt 4 (MSIT)
Expt 5 (vMSIT)
Expt 6 (Stroop)
Expt 7 (Music)

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 required 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 artificial, 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 naïve 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).

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Language and Verbal WM

Language-selective portion of the LIFG language ROI

Language and Stroop

Language-selective portion of the LIFG language ROI

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. 51) and (ii) individual subjects’ localizations maps thresholded at P < 0.001, uncorrected.

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, a sample of 10 out of 20 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 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 version) 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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