Complementary hemispheric lateralization of language and social processing in the human brain

Graphical abstract

Highlights
- Cortical activation maps in language and social tasks show a striking similarity
- Language and social activations are lateralized to left and right brain, respectively
- Homologs of language areas in the right hemisphere are involved in social processing
- Outside the language network, a left-hemisphere dominance is seen in both tasks

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In brief
Rajimehr et al. demonstrate a relationship between language and social processing in the brain. While language areas are typically found in the left hemisphere, their homologs in the right hemisphere are involved in social processing. The results have implications for understanding how the cortical language network has evolved in humans.
Complementary hemispheric lateralization of language and social processing in the human brain

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SUMMARY

Humans have a unique ability to use language for social communication. The neural architecture for language comprehension and production may have prominently emerged in the brain areas that were originally involved in social cognition. Here, we directly tested the fundamental link between language and social processing using functional magnetic resonance data (MRI) data from over 1,000 human subjects. Cortical activations in language and social tasks showed a striking similarity with a complementary hemispheric lateralization. Within core language areas, left-lateralized activations in the language task were mirrored by right-lateralized activations in the social task. Outside these areas, the activations were left lateralized in both tasks, perhaps indicating multimodal integration of social and semantic information. Our findings could have important implications in understanding neurocognitive mechanisms of social disorders such as autism.

INTRODUCTION

Language is a distinctive component of human cognition. This cognitive process is mediated by a network of cortical areas in lateral temporal and lateral prefrontal cortices (Friederici, 2011), which are collectively involved in language comprehension (Fedorenko et al., 2011) and language production (Sahin et al., 2009). A classic fact about the organization of the language processing network is that the language areas are strongly lateralized to the left hemisphere (LH) in about 95% of right-handed individuals and about 75% of left-handed individuals (Knecht et al., 2000). This hemispheric specialization for language raises some fundamental questions. Is there specialization for a certain cognitive faculty in the right-hemisphere (RH) areas corresponding (homotopic) to LH language areas? If there is such specialization, does it show an opposite lateralization (i.e., RH dominance)? Do the homotopic areas of the two hemispheres have complementary functions? Does the degree of hemispheric lateralization in these areas predict performance in specific tasks?

We hypothesized that the homotopic language areas in the RH are prominently specialized for social processing. Social processing in the brain could be characterized as a set of cortical computations for (1) perceiving socially relevant stimuli such as biological motion, dynamic faces, and gaze direction (Redcay et al., 2010), (2) recognizing other people’s actions (Pelphrey et al., 2004), and (4) mental reasoning about beliefs and thoughts of other people (theory of mind) (Jamali et al., 2021). Understanding the social content of the environment is an evolutionarily old skill that is seen in many forms across the animal kingdom. For instance, brain imaging in macaque monkeys has shown a dedicated network of bilateral cortical areas in temporal and prefrontal cortices for processing social interactions (Siiva and Freiwald, 2017; Shepherd and Freiwald, 2018). One specific form of social communication is linguistic communication, and the cortical architecture for language processing may have prominently emerged in the LH within territories that were primarily involved in social processing. Thus, based on this scenario, it would be expected that the homotopic areas in the RH contain selectivity for social processing.

RESULTS

To investigate the relationship between cortical networks of language and social processing, we used fMRI data of 1,044 healthy young adults from the Human Connectome Project (HCP) database (https://www.humanconnectome.org/study/hcp-young-adult). In each subject, cortical activation maps
Figure 1. Hemispheric lateralization effects in the language and social tasks
(A and B) Group-average activation maps for the contrasts of “story versus baseline” in the language task and “social versus random” in the social task. The maps represent Cohen’s d effect size, and they are displayed on lateral and medial views of the inflated cortical surface (fs_LR surface). In each panel, the LH is shown on the left and the RH is shown on the right.

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were obtained for language (Binder et al., 2011) and social (Castelli et al., 2000; Wheatley et al., 2007) tasks. The language task consisted of story blocks and math blocks. In the story blocks, subjects were presented with brief auditory stories and answered questions about the topic of stories. In the math blocks, subjects were auditorily presented with simple arithmetic questions. In the social task, subjects were presented with short video clips of objects (squares, circles, triangles) that either interacted in some way (approaching, chasing, etc.) or moved randomly on the screen. Subjects judged whether the objects had a social interaction or not. Functional maps from all subjects were multimodally transformed to a standard cortical surface where the LH and RH were precisely registered to each other (i.e., there was a one-to-one correspondence between points/vertices of the LH and RH) (Glasser et al., 2016a). Having such correspondence was crucial for an anatomically accurate evaluation of inter-hemispheric relations over the entire cortex.

Group-average activation maps (effect size maps) for language and social tasks were obtained by comparing the “story versus baseline” and “social versus random” conditions, respectively (Figures 1A, 1B, and S1). The stimuli and task instructions of the two tasks were drastically different. However, the activation maps showed a remarkable similarity in the topography of areas activated by story and social stimuli, especially in lateral temporal and lateral prefrontal cortices. It was also evident that the language-related activations were relatively stronger in the LH, while the social-related activations were relatively stronger in the RH. To perform a detailed analysis of hemispheric lateralization within core language areas, these areas were first localized based on the group-average language map in the LH (Figures 1C and S2). The localized areas, named based on a multimodal parcellation of the cerebral cortex (Glasser et al., 2016b), included PGI, perisylvian language area (PSL), superior temporal sulcus posterior (STSp), superior temporal sulcus anterior (STSa), superior temporal gyrus anterior (STGa), superior frontal language area (SFL), STSp, and Broca’s area (areas 44, 45, and 47) (Figure 1D). PSL, which was located within the prenum temporale, could be considered part of Wernicke’s area. Most of these areas were also activated in the “story versus math” contrast—though the separation between language and default mode networks was more pronounced in the “story versus baseline” contrast (Figure S3). Previous work confirms that the language network identified by the “story versus baseline” contrast includes neurobiologically relevant and functionally coupled areas (Glasser et al., 2016b).

Next, we examined the hemispheric lateralization within core language areas. For each task and each subject, the activation map in the LH was subtracted from the activation map in the RH, then the difference maps were averaged across subjects. The difference maps would allow evaluation of lateralization regardless of idiosyncratic differences in absolute activation levels. As expected, the language areas showed LH dominance in the language task (Figures 1E and S4). Interestingly, the same areas in the RH showed a relatively higher activation to social stimuli (Figures 1F and S4). A conjunction analysis confirmed that such opposite lateralization effects were largely confined to the language areas (Figure S5).

To quantify the effects, the functional asymmetry values (LH activation minus RH activation) were averaged across vertices in each area. All areas except PGI showed a significant double-dissociation effect: LH dominance in the language task (as expected), and RH dominance in the social task (Figure 2A). The complementary hemispheric lateralization of language and social processing (greater LH activation in the language task and greater RH activation in the social task) was robustly found when the language areas were defined at various thresholds in the group-average map (Figure S6A) or in the individual-subject maps (Figure S6B). Interestingly, in both cases, the effects were stronger at higher thresholds where the most selective vertices were included in the analysis.

Based on data of individual subjects, we selected a minority group of atypical subjects (n = 29) who clearly had strong language activations in the RH (Figures 2B and 2C) and tested whether the RH laterality effect in the social task is reduced (or perhaps eliminated) in these subjects. In the group-average maps of these subjects, most of the areas included subregions showing LH dominance in the social task (Figures 2D and S7A). Importantly at the areal level, none of the areas showed RH dominance in the social task (Figure S7B)—contrary to what we observed in the group-average map of all subjects.

At the areal level, the pattern of hemispheric biases was generally consistent across areas. However, a detailed look at the fine-scale spatial organization of language and social lateralization revealed an important difference between STSp and other areas (Figure 3). Within STSp, there was a considerable overlap between subregions showing laterality effects in language and social tasks, whereas in other areas, especially within PGI, these subregions actually avoided each other (Figures 3A and 3B). In STSp, common neural populations appear to be activated by language and social tasks (see also Deen et al., 2015), and therefore, the opposite hemispheric lateralization for language and social processing may be accentuated in this area through competition for shared neural resources. This prediction was confirmed in a subsequent analysis where we systematically tested the relationship between functional asymmetry values of language and social processing across subjects (Figure 3C). STSp showed a highly significant negative correlation between language and social lateralization, meaning that subjects with stronger language activation in the left STSp tended to have stronger social activation in the right STSp. This negative correlation in STSp was observed in both right-handed and
left-handed subjects (Figure S8). PSL also showed a weak, but significant, negative correlation, while PGi showed a significant positive correlation. In other areas, there was no association between language and social lateralization.

Do the individual differences in complementary hemispheric lateralization correlate with performance in language and social tasks? We addressed this question using behavioral data of all subjects in HCP. The behavioral measures of language processing were based on scores in vocabulary comprehension and reading recognition tests (Barch et al., 2013). The behavioral measure of social processing was based on accuracy in the social task during functional imaging. For two groups of subjects with high and low performance in these behavioral metrics, we estimated language and social lateralization effects in eight language areas (Figure S9). In PGi and PSL, higher LH lateralization in the language task was linked to better performance in the language tests. In STSp and STSa, higher RH lateralization in the social task was linked to better accuracy in this task. Thus, at

Figure 2. Hemispheric lateralization for language and social processing within language areas
(A) The lateralization effects in language areas were quantified based on data of all subjects. For each subject and each task, functional asymmetry values were averaged across vertices in each area. Data were then averaged across subjects. Error bars indicate one standard error of the mean across subjects. Mean asymmetry values were significantly different from zero in all areas (false discovery rate [FDR]-adjusted p < 0.0005; t test).
(B) For each subject and each task, a lateralization index was calculated by averaging functional asymmetry values across vertices of all areas except PGi (i.e., seven areas that showed a double-dissociation effect). The scatterplot demonstrates distribution of these indices across all subjects. A group of subjects, marked with red dots, showed strong language activations in the RH. As one would expect, the prevalence of left handedness was higher in these subjects compared with the general population.
(C and D) For this group of subjects, functional asymmetry maps were obtained by subtracting RH activations from LH activations.
Figure 3. Fine-grained organization of language and social lateralization within the language areas

(A) Functional asymmetry maps within the language areas. The areal patches were selected from the maps shown in Figures 1E and 1F, and they were magnified to show fine-grained spatial organization of language and social lateralization. Note that the maximum threshold of the maps here was set at a slightly higher value (99th percentile of data instead of 98th percentile used in other figures) to allow for a better visualization of variations in the maps.

(B) Spatial overlap between language and social asymmetry maps was quantified using the Jaccard index. In each area, we selected just vertices with positive values in the language asymmetry map and took the x% most positive. Similarly, we selected just vertices with negative values in the social asymmetry map and

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least in some areas, there was an association between hemispheric lateralization and behavioral outcome. The asymmetry maps shown in Figures 1E and 1F also revealed lateralization effects outside the language network. To quantitatively evaluate the effects in all parts of cortex, we first computed functional asymmetries in the language task for all 180 cortical areas from multimodal parcellation (Glasser et al., 2016b). In this parcellation, each parcel in the LH had a corresponding parcel in the RH. Twenty-five parcels with the highest absolute values of asymmetry were then selected as regions of interest (ROIs) (Figure S10) and visualized on the cortical surface (Figure 4A). We identified eight ROIs outside the language-auditory network. When compared with resting-state networks (Ji et al., 2019), these ROIs were predominantly located within default and frontoparietal networks (Figure S11A). Although responses in these ROIs were generally negative, they could differentiate story and math stimuli (Figure S11B). Interestingly, four frontal ROIs located immediately anterior to 55b and Broca’s area showed LH dominance in both language and social tasks (Figures 4B and 4C). Furthermore, in the majority of non-language ROIs, degree of lateralization in the language task was positively correlated with degree of lateralization in the social task (Figures 4D and S12). A possible interpretation is that some LH regions outside the language network might be involved in integrating linguistic and social information.

The stimuli used in the social task had some low-level retinotopic differences, which could result in differential activations in early visual cortex. To test this possibility, we examined the root-mean-square (RMS) contrast of images in four quadrants of the visual field. We found differences between quadrants (Figure S13), which could potentially explain the apparent asymmetry patterns seen in early visual cortex of the social asymmetry map (Figure 1F). Thus, these patterns do not appear to be related to a genuine functional asymmetry for social processing.

**DISCUSSION**

The two cerebral hemispheres sometimes show complementarity of function. While the LH is more specialized in fine-grained processing of visual stimuli, the RH is more specialized in holistic processing of global form (Fink et al., 1996). In the case of category-selective areas of visual cortex, the fusiform face area (FFA) is generally right lateralized (Yovel et al., 2008; Rossion et al., 2012), whereas the visual word form area (VWFA) is better localized in the LH (Dehaene and Cohen, 2011; Behrmann and Plaut, 2013). The brain networks of language and attention also show opposite hemispheric lateralization (Cai et al., 2013). While the language areas are typically located in the LH, the RH appears to be specifically involved in the control of visuospatial attention. In all cases described above, the lateralization of a certain area/processing in one hemisphere is often accompanied by the lateralization of another area/processing in the other hemisphere. Complementary lateralization of language and social processing reported in our study is unique in the sense that the homologous areas of the two hemispheres showed such lateralization effects—with some fine-scale differentiations within the areas. A comparison of the activation maps across a wide range of cognitive tasks indicates that the homologs of language areas in the RH are selectively involved in the processing of social information—i.e., strong activations in the social task but not in the other tasks (Figures S14 and S15).

Previous studies have shown that the homologs of language areas in the RH are also involved in the processing of prosody (Wildgruber et al., 2006). Affective-prosodic components of speech play an important role in social communications, and they may tightly linked to other elements of social processing in the RH. It has also been reported that the homolog of Broca’s area (Brodmann areas 44/45) in the RH is active during the observation of hand/mouth actions performed by other individuals (Radula et al., 2006). Thus, this area, along with other areas of the “mirror-neuron” system, could encode information necessary for gestural communication (Nishitani et al., 2005). Another possibility is that this area represents social contents of actions rather than actions per se. Overall, the previously proposed functions for the RH homologs of language areas could be characterized as various forms of social processing.

It has been suggested that hemispheric lateralization has computational benefits (Kosslyn, 1987). Unilateral systems could be efficient for coordinating rapid sequences of precise, ordered operations. In fact, the degree of functional asymmetry across the two hemispheres predicts behavioral measures of verbal and visuospatial ability (Gotts et al., 2013). Such systems would also contribute to compact wiring of the brain by minimizing the aggregate length of cortico-cortical connections. Complementary hemispheric lateralization of language and social processing might be essential for a normal behavior in these domains, and it may be disrupted in autistic patients who have difficulty in both linguistic and social communications. A recent study has reported reduced language lateralization in autism (Jouravlev et al., 2020). Further studies are needed to comprehensively explore complementary lateralization of language and social processing in autistic patients. Such tests could provide new insights about the possible neurobiological causes of autism spectrum disorder.

Some regions outside the language network showed LH dominance in both language and social tasks. These regions were predominantly located within the “task-negative” default mode network. Responses in these regions were negative compared with the baseline—though they could differentiate story and math stimuli (generally a more negative response in the math task and a less negative response in the story task). A strong suppression/inhibition of default mode regions during the math task suggests that this task was cognitively more demanding. In fact, the frontoparietal multiple-demand network was highly
active in the math task (see Figure S3). The story task was apparently less demanding, as the performance of subjects was near 100%, which could allow the default mode regions to show a partial "release from suppression." This release from suppression could also be a sign that these regions have some involvement in the story task since activity in the default mode network has been associated with semantic processing, processing of contextual associations, recall from the memory, and other forms of thinking. A previous study has reported a similar profile of response in a default mode region during the perception of familiar faces (i.e., a weaker suppression of activity for familiar than unfamiliar faces), which has been attributed to the semantic/social processing of the stimuli (Silson et al., 2019). It has also been shown that the default mode network plays a role in the integration of disparate sources of information (Lanzoni et al., 2020). Thus, some default mode regions (particularly in the LH) might be involved in integrating semantic and social information.

Limitations of the study
The correlation values in our study (e.g., the negative correlation between the lateralization effects of language and social...
processing in area STSp) were relatively low. The low correlations could be due to the noisy fMRI measurements in each subject. The HCP database is unique in terms of the number of subjects tested. However, each subject has been scanned in only two functional runs for each task. Thus, given the noise in data, the correlations may not be low if they are adjusted for noise. Even if the measurement noise is minimized or adjusted, the correlations would not be perfect because there are always some atypical subjects that show a different pattern of results compared with the general population (e.g., they show similar hemispheric lateralization for the language and social processing in area STSp). These subjects may also demonstrate a different topographic organization of functional asymmetries and a different behavioral profile in the language and social tasks. A detailed investigation of individual differences in the lateralization effects could be an interesting topic for a future study.

The social task in our study revealed the cortical representations for a specific form of social processing, which was related to perceiving social interactions in visually presented stimuli. As mentioned in the introduction, social perception and cognition could have many other facets (e.g., thinking about other people’s thoughts and beliefs). Although the cortical representations for various forms of social processing may show a considerable commonality, the degree of RH dominance in the representations and its relationship with language processing need to be tested for a wide range of social tasks.

STAR METHODS

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.celrep.2022.111617.

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AUTHOR CONTRIBUTIONS

R.R. conceived the idea and designed the analyses; A.F. performed data analysis and prepared figures; H.R. and N.A. provided analysis tools; R.R. wrote the manuscript; J.D. critically revised the manuscript. All authors approved final version of the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR METHODS

KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER                      |
|---------------------|--------|---------------------------------|
| Software and algorithms |        |                                 |
| E-Prime             | Psychology Software Tools | https://pstnet.com/products/e-prime |
| Connectome Workbench | HCP    | http://www.humanconnectome.org/software/connectome-workbench.html |
| FreeSurfer          | Fischl (2012)         | https://surfer.nmr.mgh.harvard.edu |
| FSL                 | Jenkinson et al. (2012) | https://fsl.fmrib.ox.ac.uk/fsl/fslwiki |
| MATLAB              | MathWorks           | https://www.mathworks.com/products/matlab.html |
| Analysis codes and files | This paper | https://doi.org/10.5281/zenodo.7167408 |

RESOURCE AVAILABILITY

Lead contact
Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Reza Rajimehr (reza.rajimehr@mrc-cbu.cam.ac.uk).

Materials availability
This study did not generate new unique reagents.

Data and code availability
- All data used in this manuscript are part of publicly available and anonymized HCP database (https://www.humanconnectome.org).
- All original code has been deposited at Zenodo and is publicly available as of the date of publication. DOIs are listed in the key resources table.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Subjects
In this study, we used the “HCP1200” dataset (March 2017 data release) of healthy adults aged 22–35 (https://www.humanconnectome.org/study/hcp-young-adult/document/1200-subjects-data-release). The dataset included 1045 subjects. One subject (subject ID: 765864) had a large MR artifact, and this subject was excluded after consulting with the HCP team. The remaining 1044 subjects (559 females, 485 males) had complete functional data for both language and social tasks. Subjects were recruited from Washington University (St. Louis, MO) and the surrounding area. The HCP data were acquired using protocols approved by the Washington University institutional review board, and written informed consent was obtained from all subjects.

METHOD DETAILS

Task paradigm
Functional data in this study were based on the HCP language processing and the HCP social cognition (theory of mind) tasks (Barch et al., 2013).

The language task consisted of two runs (run duration = 3:57 min:sec). In each run, 4 blocks of a story task were interleaved with 4 blocks of a math task. The lengths of blocks varied, and the average duration of blocks was approximately 30 s. In the story blocks, participants were presented with brief auditory stories (5–9 sentences) adapted from Aesop’s fables, followed by a 2-alternative forced-choice question that asked participants about the topic of the story. For example, after a story about an eagle that saves a man who had done him a favor, participants were asked “That was about revenge or reciprocity?” Participants pressed a button to select either the first or the second choice. The math task also included trials that were presented auditorily. In these trials, participants completed a series of simple arithmetic (addition and subtraction) operations (e.g., “Fourteen plus twelve”), followed by...
“equals” and then two choices (e.g., “twenty-nine or twenty-six”). Participants pressed a button to select either the first or the second answer. The math task was adaptive to maintain a similar level of difficulty across participants.

In the social task, participants were presented with short video clips (20 s) of objects (squares, circles, triangles) either interacting in some way or moving randomly. After each video clip, participants were required to choose between 3 possibilities: a social/mental interaction (an interaction that appears as if the shapes are taking into account each other’s feelings and thoughts), not sure, or no interaction (i.e., there is no obvious interaction between the shapes, and the movement appears to be random). The social task consisted of two runs (run duration = 3:27 min:sec). Each run contained 5 video blocks (2 Social and 3 Random in one run, 3 Social and 2 Random in the other run) and 5 fixation blocks (15 s each).

### Data acquisition
The HCP MRI data acquisition has previously been described in detail (Glasser et al., 2013; Smith et al., 2013; Ugurbil et al., 2013). Images were acquired using a customized 3T Siemens ‘Connectom’ Skyra scanner having a 100 mT/m SC72 gradient insert and a standard Siemens 32-channel RF-receive head coil. At least one 3D T1w MPRAGE image and one 3D T2w SPACE image were acquired at 0.7 mm isotropic resolution. Whole-brain resting-state fMRI and task fMRI data were acquired using multi-band EPI sequence with parameters of TR = 720 ms, 2 mm isotropic voxels, and multi-band acceleration factor of 8. Spin echo field maps were acquired during both structural and fMRI scanning sessions to enable accurate cross-modal registration of structural and functional images in each subject.

### QUANTIFICATION AND STATISTICAL ANALYSIS

#### Analysis of structural data
Structural images (T1w and T2w) were used for extracting subcortical gray matter structures and reconstructing cortical surfaces in each subject. Volume data were transformed from native space into MNI space using a nonlinear volume-based registration. For accurate cross-subject registration of cortical surfaces, a multimodal surface matching (MSM) algorithm (Robinson et al., 2014) was used. The MSM algorithm had two versions: ‘MSMSulc’ (non-rigid surface alignment based on folding patterns) and ‘MSMAll’ (optimized alignment of cortical areas using sulcal depth maps plus features from other modalities including myelin maps, resting-state network maps, and visuotopic connectivity maps). Data in our work were based on MSMAll registration. After surface and volume registration, cortical vertices were combined with subcortical gray matter voxels to form the standard ‘CIFTI grayordinates’ space (91,282 vertices/voxels with ~2 mm cortical vertex spacing and 2 mm isotropic subcortical voxels) (Glasser et al., 2016a).

#### Analysis of fMRI data
Functional images were minimally preprocessed using the HCP pipelines (Glasser et al., 2013). Preprocessing included correction for spatial distortions due to gradient nonlinearity and B0 field inhomogeneity, fieldmap-based unwarping of EPI images, motion correction, brain-boundary-based registration of EPI to structural T1w scans, non-linear registration to MNI space, and grand-mean intensity normalization. Data from the cortical gray matter ribbon were projected onto the surface and then onto the standard grayordinates space. Data were minimally smoothed by a 2mm FWHM Gaussian kernel in the grayordinates space. Thus, smoothing was constrained to the cortical surface mesh in each hemisphere. Data were cleaned up for artifacts and structured noise using sLOQ + FIX.

The preprocessed functional time-series were entered into a general linear model (GLM) to estimate functional activities in each vertex/voxel in each run (Barch et al., 2013). Two regressors/predictors were included in the GLM design of the language task – Story and Math. Each predictor covered the duration of a block (~30 s). Two regressors/predictors were included in the GLM design of the social task – Social and Random. Each predictor covered the duration of a single video clip (20 s). The regressors in the social task were defined based on the presented stimuli (not the subjects’ responses). All regressors were convolved with a canonical hemodynamic response function and its temporal derivatives. The time-series were temporally filtered with a Gaussian-weighted linear high-pass filter with a cutoff of 200 s, to remove low-frequency drifts/fluctuations presumably unrelated to the task design. The time-series were also prewhitened to remove temporal autocorrelations in the fMRI signal. For three comparisons ('story vs. baseline', ‘story vs. math’, and ‘social vs. random’), the contrast of parameter estimate (COPE) was computed based on beta values of the GLM. The language task did not have typical fixation blocks (there was only an 8-second ‘get ready’ countdown at the beginning of the run), and the baseline condition in this task represented the mean activity across all time-points in each run. Fixed-effects analyses were conducted to estimate the average effects across runs within each subject, then mixed-effects analyses treating subjects as random effects were conducted to obtain group-average maps. The group-average maps were Cohen’s d effect size maps. Cohen’s d in each vertex/voxel was computed as the mean COPE (across subjects) divided by the standard deviation. For thresholding, vertices with positive Cohen’s d values were first selected, then the mean value across these vertices was used as the threshold. After binarizing, a multi-modal parcellation of cerebral cortex (Glasser et al., 2016b) was overlaid on the thresholded map to identify the auditory cortex (low-level and high-level auditory regions), divide the superior temporal region, and name activated language areas.