Title: Functionally distinct language and Theory and Mind networks work together, especially during language comprehension

Abbreviated title: Language and Theory of Mind networks

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Abstract

Communication requires the ability to generate and interpret linguistic signals, as well as the ability to infer the beliefs, desires, and goals of others (“Theory of Mind”, ToM). These two abilities have been shown to dissociate: on the one hand, individuals with severe aphasia retain the ability to think about others’ mental states; on the other hand, individuals with autism spectrum disorders are impaired in their social reasoning, but their basic language processing is often intact. In line with this evidence from developmental and acquired disorders, fMRI studies have shown that linguistic and ToM abilities are implemented in distinct sets of brain regions. And yet, language is fundamentally a social tool that allows us to share thoughts with one another. Thus, the language and ToM networks should work closely together in spite of being implemented in distinct neural circuits. Here, we investigated potential interactions between these networks during naturalistic cognition using the functional correlation approach in fMRI. Although inter-region correlations within each network were higher than between-network correlations across experiments, we also observed reliably above-baseline synchronization of BOLD signal fluctuations between the two networks during rest and, to an even greater extent, during story comprehension. This synchronization was functionally specific: neither network synchronized with the executive control network. Thus, coordination between the language and ToM networks appears to be an inherent characteristic of their functional architecture, and is increased during naturalistic language processing.

54 **New and Noteworthy**

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56 Humans differ from non-human primates in their abilities to communicate linguistically, and to
57 infer others' mental states. Although linguistic and social abilities appear to be interlinked onto-
58 and phylo-genetically, they are dissociated in the adult human brain. Yet successful
59 communication requires language and social reasoning to work together. Using fMRI, we show
60 that language regions synchronize significantly with social regions during rest, and even more
61 during language comprehension, identifying a possible mechanism for network interaction.

Introduction

Language is the primary means for human interaction, and communicative success requires an ability to reason about a conversation partner's beliefs, desires, and goals (e.g., Grice 1957, 1968, 1975; Sperber & Wilson, 1986). This ability to make inferences about others' mental states is often referred to as "mentalizing" or "Theory of Mind (ToM)". Two kinds of evidence suggest that in a mature human brain the cognitive and neural mechanisms that support ToM reasoning are dissociated from basic language processing mechanisms. *First*, patients with aphasia experience significant difficulty understanding and/or producing language, but appear to be largely unimpaired in their ToM reasoning (e.g., Dronkers et al., 1998; Varley & Siegal, 2000; Varley, Siegal & Want, 2001; Apperly et al., 2006; Willems et al., 2011). Conversely, individuals with autism spectrum disorders suffer from ToM – or more generalized social – deficits (e.g., Baron-Cohen et al., 1985; Happé, 1993), yet often have their core linguistic processing abilities intact (e.g., Tager-Flusberg, Paul & Lord, 2005; Wilkinson, 1998; Lord & Paul, 1997; Tager-Flusberg, 2006; Asberg, 2010; Terzi, Marinis, & Francis, 2016; Diehl, Bennetto, Young, 2006; Janke, Perovic, 2015; Frith & Happe, 1994). And *second*, neuroimaging studies with healthy adults have revealed that largely distinct sets of brain regions support ToM vs. language processing abilities. Specifically, ToM reasoning engages bilateral regions at the junction of temporal and parietal lobes, and a set of regions along the cortical midline (e.g., Fletcher et al., 1995; Gallagher et al., 2000; Vogeley et al., 2001; Ruby and Decety, 2003; Saxe and Kanwisher, 2003; Ciaramidaro et al., 2007; Gobbini et al., 2007; Jacoby et al., 2016; see e.g., Saxe & Young, 2016, for a review). In contrast, language processing engages a set of regions on

the lateral surfaces of left frontal and temporal lobes (e.g., Binder et al., 1997; Fedorenko et al., 2010, 2011).

Notwithstanding the evidence for distinct cognitive and neural mechanisms for ToM reasoning and language processing, there are reasons to postulate a deep connection between them. First, much of what people talk about either directly *concerns mental states*, or requires *mental state inference* from information about the physical world (e.g., Dunbar, 1994; Emler, 1994; Dunbar et al., 1997; Feinberg et al., 2012). Second, most linguistic exchanges go beyond the literal meaning of the utterance and require *pragmatic reasoning* on the side of both producer and comprehender, which involves ToM inference of communicative intentions (e.g., Grice 1957, 1968, 1975; Sperber & Wilson, 1986; Clark & Wilkes-Gibbs, 1986; Benz et al., 2006; Frank & Goodman, 2012; Goodman & Frank, 2016). Third, some aspects of language appear critical for the *development of ToM abilities*. For example, training children with no understanding of false beliefs on certain words or constructions allows them to pass tests of false belief understanding (e.g., Appleton & Reddy, 1996; Slaughter & Gopnik, 1996; Clements et al., 2000; Hale & Tager-Flusberg, 2003; Lohmann & Tomasello, 2003). And fourth, human language has been shown to be shaped by the social *communicative pressures* to optimize information transfer at all levels, from the sound structure (e.g., Maddieson & Disner 1984; Maddieson & Ladefoged 1996), to the lexicon (e.g., Zipf, 1949; Piantadosi et al., 2011; Dautriche et al., 2016; Blasi et al., 2016), to grammar (e.g., Kirby, 2000; Smith et al., 2003; Gibson et al., 2013; Futrell et al., 2015; Levinson, 2016).

Given their intimate relationship, the ToM and language systems must have a way to interact with each other. Indeed, Deen et al. (2015) reported a small amount of overlap between language and ToM activations in left superior temporal cortex. However, another – possibly

complementary – way to implement inter-system interaction is via synchronization in neural activity between the regions of one system and those of the other system (e.g., Cole et al, 2013). Here we use fMRI to ask whether the language and ToM networks exhibit such synchronization during naturalistic cognition.

Methods

Participants. Twenty-six right-handed native English speakers (age 18-31, 5 males) from MIT and the surrounding Cambridge community participated for payment. Fifteen participants took part in Experiment 1a (resting state). The same participants, plus one further participant, took part in Experiment 1b (story comprehension); and ten different participants took part in Experiment 2 (story comprehension, replication). All participants gave informed consent in accordance with the requirements of MIT’s Committee on the Use of Humans as Experimental Subjects (COUHES).

General approach. The experiments were designed to assess the degree of synchronization between the language and ToM networks, as well as whether this synchronization is specific to language and theory of mind and not a general property of any pair of large-scale networks. Each participant completed a critical task (resting state and/or story comprehension), and three functional “localizer” tasks (e.g., Saxe et al., 2006; Nieto-Castañón & Fedorenko, 2012): a language network localizer (Fedorenko et al., 2010), a ToM network localizer (Saxe & Kanwisher, 2003), and an additional localizer for the domain-general multiple demand (MD) network (Duncan, 2010; Fedorenko et al., 2013). These three localizers were used to define three sets of functional regions of interest (fROIs), separately in each individual brain.

BOLD signal time-courses during the critical tasks were then extracted from these fROIs and their degree of synchronization across regions was measured, as detailed below. The MD network localizer was included to a) allow for a replication of an earlier reported dissociation between the language and the MD network (Blank et al., 2014), in line with current emphasis in the field on replicability (e.g., Poldrack et al., 2017), and b) assess the specificity of the language-ToM system association by testing the relationship between the ToM system and the MD system.

Design, stimuli, and procedure.

Language localizer task. The task used to localize the language network is described in detail in Fedorenko et al. (2010) and targets brain regions that support high-level language processing, including both lexical-semantic and combinatorial (semantic and syntactic) processes (e.g., Fedorenko et al., 2012; Bautista & Wilson, 2016; Blank et al., 2016). It also identifies right-hemisphere homologues of the classic, left-lateralized language regions (e.g., Mahowald & Fedorenko, 2016), which have been proposed to participate in pragmatic reasoning (e.g., Joannette et al., 1990; Kuperberg et al., 2000; Coulson & Williams, 2005; Mashal et al., 2005; Eviatar et al., 2006; Diaz et al., 2011). Briefly, we used a reading task that contrasted sentences (the critical condition) and lists of unconnected, pronounceable nonwords (the control condition; Figure 1) in a standard blocked design with a counterbalanced order across runs (for timing parameters, see Table 1). Stimuli were presented one word / nonword at a time. For the participants in Experiment 2, each trial ended with a memory probe, and they had to indicate, via a button press, whether or not that probe had appeared in the preceding sentence / nonword sequence. The remaining participants read the materials passively (for these participants, we included a button-

press task at the end of each trial, to maintain alertness). This localizer contrast has been shown to generalize across materials, tasks (e.g., Fedorenko et al., 2010; Scott et al., 2016), and visual/auditory presentation (e.g., Fedorenko et al., 2010, Braze et al., 2011; Vagharchakian et al., 2012). For example, Scott et al. (2016) showed that a contrast between speech excerpts and acoustically degraded speech elicits the same effect. Each participant completed between two and four runs. (A version of this localizer is available from <http://https://evlab.mit.edu/funcloc/download-paradigms>.)

ToM localizer task. The task used to localize the ToM network is described in detail in Saxe & Kanwisher (2003) and targets brain regions that support reasoning about others' mental states. Briefly, the task was based on the false belief paradigm, a classic paradigm in ToM research (Wimmer and Perner, 1983), and contrasted verbal vignettes about false beliefs (e.g., a protagonist has a false belief about an object's location; the critical condition) and false physical states (physical representations depicting outdated scenes, e.g., a photograph showing an object that has since been removed; the control condition). Participants read these vignettes, one at a time, in a long-event-related design with a counterbalanced order across runs. Each vignette was followed by a true / false comprehension question. Eighteen participants completed two runs and eight completed one run due to time limitations, each lasting 262s and consisting of 5 vignettes per condition. (A version of this localizer is available from <http://saxelab.mit.edu/superloc.php>.)

MD localizer task. The spatial working memory task used to localize the MD network is described in detail in Fedorenko et al. (2013; see also Blank et al., 2014) and targets brain regions sensitive to general executive demands (see Duncan & Owen, 2000, Fedorenko et al., 2013, and Hugdahl et al., 2015, for evidence that diverse demanding tasks activate this network). On each trial, participants saw a 3×4 grid and kept track of eight (hard version; the critical

condition) or four (easy version; the control condition) locations that were sequentially flashed two at a time or one at a time, respectively. Then, participants indicated their memory for these locations in a two-alternative, forced-choice paradigm via a button press. Feedback was provided after every trial. Hard and easy conditions were presented in a standard blocked design (4 trials in a 32s block, 6 blocks per condition per run) with a counterbalanced order across runs. Each run included 4 blocks of fixation (16s each) and lasted a total of 448s. Twenty-four participants completed two runs and two completed one run due to time limitations. (This localizer is available from the authors upon request.)

Critical tasks. In the resting state experiment, participants were instructed to close their eyes and let their mind wander but to remain awake while resting in the scanner for 5 min (the scanner lights were dimmed and the overhead projector was turned off). In the story comprehension experiments, participants listened to stories (5 stories each in Experiment 1b; 4-8 stories in Experiment 2) over scanner-safe headphones (Sensimetrics, Malden, MA). Stories lasted between 4.5 and 6 min. They were adapted from existing, publicly available texts (fairy tales and short stories). The stories were recorded by two native English speakers (a male and a female). The stories were rich in mental state content (Table 2; the complete materials are available at <http://github.com/languageMIT/naturalstories>). To ensure deep understanding, following the scan for each story, participants answered twelve (Experiment 1) or six (Experiment 2) comprehension questions, presented in a two-alternative forced-choice format. For four participants, the behavioral data were lost due to equipment malfunction. For each of the remaining participants, accuracy on these questions was significantly above chance, as indicated by the binomial test (for all tests, $p < 0.04$; mean accuracy across participants: 82.22%, SD: 10.8).

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200 *Data acquisition and preprocessing.*

201 *Data acquisition.* Structural and functional data were collected on a whole-body 3 Tesla
 202 Siemens Trio scanner with a 32-channel head coil at the Athinoula A. Martinos Imaging Center
 203 at the McGovern Institute for Brain Research at MIT. T1-weighted structural images were
 204 collected in 176 axial slices with 1mm isotropic voxels (repetition time (TR) = 2,530ms; echo
 205 time (TE) = 3.48ms). Functional, blood oxygenation level-dependent (BOLD) data were
 206 acquired using an EPI sequence with a 90° flip angle and using GRAPPA with an acceleration
 207 factor of 2; the following parameters were used: thirty-one 4.4mm thick near-axial slices
 208 acquired in an interleaved order (with 10% distance factor), with an in-plane resolution of 2.1mm
 209 $\times$ 2.1mm, FoV in the phase encoding (A $\gg$ P) direction 200mm and matrix size 96mm $\times$ 96mm,
 210 TR = 2000ms and TE = 30ms. The first 10s of each run were excluded to allow for steady state
 211 magnetization.

212 *Spatial preprocessing.* Data preprocessing was carried out with SPM5 and custom
 213 MATLAB scripts. Preprocessing of anatomical data included normalization into a common
 214 space (Montreal Neurological Institute (MNI) template, resampling into 2mm isotropic voxels,
 215 and segmentation into probabilistic maps of the gray matter, white matter (WM) and
 216 cerebrospinal fluid (CSF). Preprocessing of functional data included motion correction,
 217 normalization, resampling into 2mm isotropic voxels, smoothing with a 4mm FWHM Gaussian
 218 kernel and high-pass filtering at 200s.

219 *Temporal preprocessing.* Additional preprocessing of data from the resting state and
 220 story comprehension runs was carried out using the CONN toolbox (Whitfield-Gabrieli and
 221 Nieto-Castañón, 2012) with default parameters, unless specified otherwise. Five temporal

principal components of the BOLD signal time-courses extracted from the WM were regressed out of each voxel's time-course; signal originating in the CSF was similarly regressed out. Six principal components of the six motion parameters estimated during offline motion correction were also regressed out, as well as their first time derivative. Next, as in Blank et al. (2014), the residual signal was bandpass filtered (0.008–0.09 Hz) to preserve only low-frequency signal fluctuations (Cordes et al., 2001). (As in Blank et al. (2014), the general pattern of results was similar without bandpass filtering (see also Gohel & Biswal, 2015).)

Modeling localizer data. For each localizer task, a general linear model estimated the effect size of each condition in each experimental run in each voxel. These effects were each modeled with a boxcar function (representing entire blocks/events) convolved with the canonical Hemodynamic Response Function (HRF). The model also included first-order temporal derivatives of these effects, as well as nuisance regressors representing entire experimental runs and offline-estimated motion parameters. The obtained beta weights were then used to compute the functional contrast of interest: sentences > nonwords for the language localizer, false belief > false physical for the ToM localizer, and hard > easy spatial working memory for the MD localizer.

Defining functional regions of interest (fROIs). For each participant, functional ROIs were defined by combining two sources of information (Fedorenko et al. 2010; Julian et al. 2012): 1) the participant's activation map for the relevant localizer contrast, and 2) group-level constraints ("masks"). The latter demarcated brain areas within which most or all individuals in prior studies showed activity for the localizer contrasts (Figure 2).

For the language fROIs, we used masks derived from a group-level representation for the sentences > nonwords contrast in a set of 220 participants. These masks (available for download

from http://web.mit.edu/evelina9/www/funcloc/funcloc_parcel.html) were similar to the masks derived from 25 participants, as originally reported in Fedorenko et al. (2010), and covered extensive portions of the left lateral frontal, temporal, and parietal cortices. In particular, six masks were used: three in the frontal lobe (LIFGorb, LIFG, LMFG), and three in the temporal and parietal cortices (LAntTemp, LPostTemp, and LAngG).

Although in the main analysis we were interested in the left hemisphere (LH) language regions, we additionally defined the right hemisphere (RH) homolog of the language network. To do so, the LH masks were mirror-projected onto the RH to create six homologous masks. By design, the masks (Figure 2) cover large swaths of cortex in order to be able to accommodate inter-individual variability. Hence the mirrored versions are likely to encompass RH language regions despite possible hemispheric asymmetries in the precise locations of activations (see Mahowald & Fedorenko, 2016, for evidence). We included RH language regions because they have been argued to support some aspects of pragmatic / communicative processing (e.g., Joannette et al., 1990; Kuperberg et al., 2000; Coulson & Williams, 2005; Mashal et al., 2005; Eviatar et al., 2006; Diaz et al., 2011). One may therefore hypothesize that RH language fROIs would show greater synchronization than LH language fROIs with the regions of the ToM network. We evaluated this hypothesis in one of the analyses.

For the ToM fROIs, we used masks derived from a group-level representation for the false belief > false physical contrast in an independent group of 462 participants (Dufour et al., 2013). These masks (available for download from <http://saxelab.mit.edu/ToMgroupMaps.php>) included regions in the left and right temporo-parietal junction, left and right precuneus / posterior cingulate cortex, and left and right dorsal, middle, and ventral prefrontal cortex, for a total of 10 regions (5 per hemisphere).

For the MD fROIs, following Fedorenko et al. (2013) and Blank et al. (2014), we used anatomical masks (Tzourio-Mazoyer et al. 2002) that correspond to brain regions linked to MD activity in prior work. These masks included regions in the opercular IFG, MFG, including its orbital part, insular cortex, precentral gyrus, supplementary and presupplementary motor area, inferior and superior parietal cortex, and anterior cingulate cortex, for a total of 18 regions (9 per hemisphere). (We note that functional masks derived for the MD network based on 197 participants, available at <https://evlab.mit.edu/funcloc/download-parcels>, overlapped closely with the anatomical masks used here; we chose to use the anatomical masks in order to maintain comparability between our functional data and those from Blank et al. (2014).)

These group-level masks, in the form of binary maps, were used to constrain the selection of subject-specific fROIs. In particular, for each participant, 12 language fROIs were created by intersecting the language masks with each participant's unthresholded t -map for the sentences > nonwords contrast. For each participant and each mask, the 10% of voxels with the highest t values in the intersection image were chosen as the fROI (note that the voxels included in the RH fROIs were not constrained to be mirrored versions of their LH counterparts, but were only constrained to land within a mirrored version of the masks). In a parallel fashion, 10 ToM fROIs and 18 MD fROIs were created by intersecting the ToM and MD masks with each participant's unthresholded t -map for the false belief > false physical and hard > easy spatial working memory contrasts, respectively, and selecting the 10% of voxels with the highest t values within each mask. Finally, because our focus was on inter-system synchronization, we excluded voxels that were included in more than one fROI due to (small amounts of) spatial overlap between activation maps (e.g., Deen et al., 2015; see Blank et al., 2014, for a similar approach). The overlaps of the MD network with the language and ToM network were negligible. For the

language system, overlapping voxels accounted for 0.41% of language fROIs and 0.18% of MD fROIs (5.5 voxels on average across participants); for the ToM network, they accounted for 0.09% of ToM fROIs and 0.04% of MD fROIs (1.31 voxels on average). The overlap between language and ToM activations was higher, but still small (similar to Deen et al., 2015): overlapping voxels accounted for 4.23% of language fROIs and 3.87% of ToM fROIs (57.46 voxels on average). These overlapping voxels were localized to the bilateral posterior temporal and parietal regions: PostTemp and AngG fROIs in the language network, and TPJ fROIs in the ToM network. No voxels overlapped across all three networks. On average, a total of 64.27 voxels per participant were excluded, comprising 0.9% of our original fROI sizes.

The definition of fROIs as the 10% of voxels with the highest t values for a localizer contrast within a given mask balances the trade-off between 1) choosing only voxels that respond robustly to the relevant localizer contrast (sentences > nonwords, false belief > false physical, or hard > easy spatial working memory), and 2) having a sufficient number of voxels in the fROI. In addition, this procedure ensures that each fROI is constant in size across participants. Blank et al. (2014) compared this procedure to an alternative one, where fROIs were defined by intersecting language and MD masks with thresholded t -maps (at $p < 0.001$ uncorrected whole-brain level) for the language and MD contrasts, and obtained similar results.

Before proceeding to the critical analyses, we ensured that the fROIs showed the expected functional signatures with respect to the localizer conditions (Figure 3). To this end, the reliability of each localizer contrast effect, i.e., the difference between the regression coefficient estimates for its critical and control conditions, was tested via a two-fold, leave-n-out cross-validation across runs: for each participant, we defined fROIs based on the even localizer run(s) and then derived independent estimates of the localizer contrast effect in these fROIs based on

the odd run(s) and vice versa. The contrast effect estimates were averaged across the two partitions and tested for significance across participants (Bonferroni corrected for the number of regions within each network). Participants who only performed a single run of the MD localizer ($n=2$) or a single run of the ToM localizer ($n=8$) were excluded from this analysis (but their whole-brain activation maps were visually examined to ensure that expected activation patterns obtained). The localizer effects were highly reliable in all fROIs: LH language fROIs ($t_{(25)} > 7.48$, $ps < 10^{-5}$), RH language fROIs ($t_{(25)} > 5.36$, $ps < 10^{-4}$), ToM fROIs ($t_{(17)} > 6.39$, $ps < 10^{-4}$), and MD fROIs ($t_{(23)} > 4.79$, $ps < 0.002$).

Critical functional correlation analysis. For each fROI of each participant, we obtained a single BOLD signal time-course by averaging the voxel-wise timecourses across all voxels. For each pair of fROIs, a Pearson's product-moment correlation was computed between their timecourses. These correlations were Fisher-transformed to improve normality (Silver & Dunlap, 1987), and the fROI-to-fROI correlation coefficients were averaged to get within-network correlations for each network and between-network correlations for each pair of networks. Note that this averaging, aimed at testing the key hypotheses concerning network interactions, was performed across the (Fisher-transformed) correlation coefficients, not across the fROI timecourses. For within-network correlations, correlation-coefficient averages were computed across all pairs of the 6 LH language fROIs (15 pairs), 10 ToM fROIs (45 pairs), and 18 MD fROIs (153 pairs). In some analyses, we further include RH language fROIs (15 pairs) or all 12 LH and RH language fROIs (66 pairs). The same procedure was then repeated for between-network correlations. For the story comprehension condition, the resulting correlations were further averaged across stories within each participant prior to statistical testing.

In order to assay the patterns of functional correlations that characterize the networks and

their potential interactions, we performed (1) a series of tests of difference from baseline; and (2) paired-sample t -tests. For all tests of difference from baseline, we compared the observed sample mean correlations against empirically estimated null distributions rather than performing conventional one-sample t -tests. Specifically, rather than estimating the probability that the observed sample means were drawn from a t -distribution defined by a mean of zero and $n-1$ degrees of freedom, we estimated the probability that they were drawn from a Gaussian null distribution with parameters (mean and standard deviation) estimated from the data (e.g., Lerner et al., 2011, Blank et al., 2014). Null parameters were estimated for each computed correlation: per fROI-to-fROI correlation, per participant and, in the story comprehension experiments, per story. For each pairwise correlation, the null estimation proceeded by Fourier transforming one fROI's timecourse, shuffling the signal's phases in the frequency domain (i.e., sampling uniformly with replacement from the signal phases and randomly assigning them to frequencies), transforming the signal back to the time domain and correlating it with the intact timecourse of the second fROI (Theiler et al., 1992). This was repeated 1,000 times for each correlation, and the null mean and standard deviation were fitted to the resulting distribution of (Fisher-transformed) correlation coefficients. In order to perform group-level network-wise random effects tests, we aggregated the estimated null parameters across fROI pairs and across stories in the story comprehension experiments by averaging the means and pooling the standard deviations. The main advantage of this randomization approach is that it makes fewer assumptions about the sampling distribution than the conventional t -test, namely, it allows the parameters to be estimated from the data.

For visualization purposes, we also created three group-level matrices of fROI-to-fROI correlations, one for each experiment (Figure 4). Specifically, the Fisher-transformed correlation

between each pair of fROIs was averaged across participants (the Fisher transform decreases the bias in averaging; Silver & Dunlap, 1987), and the resulting average correlations were then inverse Fisher transformed. However, to ensure that the patterns of functional correlations reported here were observed consistently across individual participants, all two-sample *t*-tests were performed over participant-level correlations. Only the hierarchical clustering analysis (see below) relied on group-level average correlations.

Hierarchical clustering. Hierarchical clustering was performed to examine whether the functional organization of the fROIs into networks could be recovered in a data-driven way, by asking whether, based on patterns of region-to-region correlations, a) the regions would cluster together into their corresponding networks, and b) whether the language and ToM networks would show a higher degree of similarity with each other than with the MD network.

Hierarchical clustering is an algorithm that creates a binary tree structure connecting elements in a set, such that the length of branches on the tree approximates the distances among the elements, as provided by the user (Hartigan, 1975). The clustering together of elements, whose connecting path on the tree is shorter than a chosen length, therefore creates a partition of the element set without pre-specifying the number of resulting clusters (in contrast to other common methods, such as *k*-means clustering). We performed hierarchical clustering on our fROIs, providing the group-level fROI-to-fROI correlation matrix as input so that the distance between two fROIs was defined as one minus their correlation. Clustering was based on average linkage so that two clusters were merged into a bigger cluster based on the mean distance between their respective members.

The optimal partition of fROIs, based on the resulting tree, was identified via a measure of modularity (Newman & Girvan, 2004). First, by gradually decreasing the path length used as a

criterion for clustering fROIs, we generated the set of all possible partitions licensed by our hierarchical clustering solution (the longest path length generates a single cluster consisting of all 40 fROIs; the shortest path length generates 40 singleton clusters). Then, for each partition, we computed a reformulated modularity measure that is appropriate for detecting clusters in correlated data (Gómez et al., 2009). High modularity values indicate clustering solutions where, within each cluster, the positive functional correlations are stronger (and the negative functional correlations are weaker) compared with what is expected under a null model. The null model is a random fROI-to-fROI correlation matrix that preserves, for each fROI, the sum of its positive correlations and the sum of its negative correlations with the other fROIs.

Results

Figure 4 shows correlation matrices for the resting state (Experiment 1a) and story comprehension (Experiment 1b and 2) conditions. The cells' colors represent group-averaged Pearson's correlations between pairs of language, ToM, and MD fROIs, within and across networks, computed on timecourses of BOLD signal fluctuations. Prior to any network-wise statistical tests on these correlations (below), visual examination of the matrices already makes the key patterns clear. First, each of the three networks is internally integrated: pairs of fROIs within a network are strongly and positively correlated with each other. This replicates the pattern observed by Blank et al. (2014) for the language and MD networks, and extends the findings to ToM fROIs: the ToM network is also characterized by low-frequency synchronization among its constituent regions, both at rest and during the processing of rich naturalistic stimuli (see also Mason et al, 2008; von dem Hagen et al., 2013; Spreng et al, 2009;

Buckner et al., 2008; Yeo et al., 2011). Second, we replicate the dissociation between the language and MD networks reported by Blank et al. (2014): pairs of fROIs across these networks show uncorrelated activity both at rest and during story comprehension. Third and critically, many pairs of language and ToM fROIs show significant positive correlations, indicating some degree of functional association between the two networks. Further, these correlations appear to be stronger during story comprehension. Importantly, the ToM network does not appear to be positively correlated with *all* large-scale brain networks: specifically, the ToM and MD networks are not correlated, or slightly anti-correlated in their activity. These observations thus suggest a functional architecture comprised of three functionally separable networks, two of which – language and ToM networks – are characterized by some degree of functional synchronization. We now quantitatively evaluate these and some additional observations through a series of tests on the average pairwise correlations within and across networks.

i. The internal architecture of each of the three networks.

First, we tested the hypothesis that each of the networks is internally integrated by conducting one-sample *t*-tests on within-network correlations against empirical baselines, estimated via phase-shuffling of the BOLD time courses (see Methods). We performed separate tests per hemisphere, as well as tests of the inter-hemispheric correlations for each network. The results, summarized in Table 3, show that all average within-network correlations are highly significant ($p < 10^{-7}$, Bonferroni-corrected for multiple comparisons, here and for all that follows; here, 9 comparisons for Experiments 1a/b, and 6 comparisons for Experiment 2), consistent with the hypothesis that these networks are each internally integrated. To reduce the number of comparisons in the following analyses, we focus on the classical, left-hemisphere language

fROIs (returning to the right hemispheric fROIs in section iii), and collapse across left- and right-hemisphere fROIs for the bilateral ToM and MD networks (6 comparisons for Experiment 1a/b, and 3 comparisons for Experiment 2).

ii. What is the relationship between the language and the ToM networks?

To test our critical hypothesis – that the language network and the ToM network are functionally associated – we tested the language-ToM correlation against baseline. We observed a significant positive correlation, both at rest in Experiment 1a (mean $r = 0.125$, $SD = 0.14$ across participants, $p = 0.024$) and during story comprehension in Experiment 1b (mean $r = 0.258$, $SD = 0.1$, $p < 10^{-10}$). The latter result was reproduced in the replication sample in Experiment 2 (mean $r = 0.228$, $SD = 0.08$, $p < 10^{-5}$). In contrast, and replicating Blank et al. (2014), the language-MD correlations did not significantly differ from baseline (rest, Experiment 1a: mean $r = 0.055$, $SD = 0.113$, n.s.; stories, Experiment 1b: mean $r = -0.042$, $SD = 0.079$, n.s.). It is important to note that this pattern of between-network correlations for language-ToM and language-MD is not due to inter-region distances being, on average, shorter for pairs of language and ToM regions than for pairs of language and MD regions: in fact, inter-region distances are quite similar (language-ToM average distance between the mask centroids: 85.24mm, language-MD average distance: 81.19mm; $t(334) = 1.18$, $p = 0.24$). Finally, the ToM network and the MD network were marginally anti-correlated at rest (Experiment 1a: mean $r = -0.108$, $SD = 0.131$, $p = 0.075$) and significantly anti-correlated during story comprehension (Experiment 1b: mean $r = -0.131$, $SD = 0.102$, $p = 0.005$).

Next we tested whether the language and ToM networks are dissociable despite their significant positive between-network correlations, by performing paired-sample t -tests

comparing the within-network language and ToM correlations against the between-network language-ToM correlation. In both the resting state and story comprehension conditions, we found significantly lower language-ToM correlations than within-language correlations (rest, Experiment 1a: $t(14) = -6.223$, $p < 10^{-4}$; stories, Experiment 1b : $t(15) = -14.995$, $p < 10^{-9}$) and within-ToM correlations (rest: $t(14) = -6.647$, $p < 10^{-4}$; stories: $t(15) = -7.578$, $p < 10^{-5}$). The same pattern was observed in the story comprehension replication sample in Experiment 2, for both the within-language *vs.* language-ToM correlations, ($t(9) = 11.053$, $p < 10^{-5}$) and the within-ToM *vs.* language-ToM correlations, ($t(9) = 8.862$, $p < 10^{-5}$). Therefore, although the language and ToM networks appear to be functionally coupled, they remain dissociable both at rest and during story comprehension.

Finally, we tested whether the language-ToM synchronization was reliably stronger during story comprehension compared to rest in a set of participants in Experiment 1a who were also tested in Experiment 1b ($n=15$). (Note that although it is true that Experiment 1b – the stories condition – has more data than Experiment 1a – the rest condition – the amount of data should not affect the observed *sizes* of the correlations, only the within-subject reliability of the estimates. As a result, this comparison is reasonable.) Indeed, the language-ToM correlation was significantly higher during story comprehension ($t(14) = 4.313$, $p = 0.004$), suggesting that the two networks increase online coordination during the processing of rich naturalistic stimuli, perhaps especially stimuli that place high demands on both linguistic and social processing. Interestingly, the increase in online coordination during the processing of such stimuli is not a general property of every two high-level networks. In particular, the language-MD and ToM-MD correlations actually *decreased* numerically between rest and story comprehension, albeit non-significantly ($t(14) = -2.969$, $p = 0.061$, and $t(14) = -0.890$, *n.s.*, respectively). When looking at

changes in the within-network correlations, we observed a significant increase for the language and MD networks during story comprehension relative to rest ($t(14) = 4.266, p = 0.005$, and $t(14) = 3.574, p = 0.018$), and a marginal one for the ToM network ($t(14) = 2.998, p = 0.058$).

(Because our sample was not sex-balanced, with a higher proportion of females, we examined the distribution of individual participants' data points broken down by sex (Figure 8). As expected, given robust similarities in neural architecture between males and females (e.g., Frost et al., 1999; Sommer et al., 2004; Haut & Barch, 2006; Plante et al., 2006), the results looked similar across the two groups.)

iii. Potential hemispheric differences in the language-ToM network relationship.

We have so far focused on the classic LH language network, given that the LH language regions have been causally implicated in language processing with damage to these regions in adulthood resulting in deficits in language production and/or comprehension (e.g., Penfield & Roberts, 1959; Whitaker & Ojemann, 1977; Bates et al., 2003; Mesulam et al., 2015; Mirman et al., 2015; Fridriksson et al., 2016). However, the RH homolog of the language network has received a lot of attention in the literature over the years, and in ways relevant to the question investigated in the current study. In particular, RH language regions have been implicated in some aspects of non-literal language processing and pragmatic reasoning, which involves the computation of speakers' *intended* meanings (e.g., Joanette et al., 1990; Kuperberg et al., 2000; Coulson & Williams, 2005; Mashal et al., 2005; Eviatar et al., 2006). One might therefore hypothesize that these regions would have an even stronger relationship with the ToM network than the LH language regions. To test this hypothesis, we examined the LH and RH language network separately. At rest, the average correlation of the RH language fROIs with the ToM network did

not significantly differ from that of the LH language fROIs ($t(14) = 0.665$, *n.s.*; Figure 6). During story comprehension, it was significantly weaker in Experiment 1b ($t(15) = 2.882$, $p = 0.011$) and did not differ from the LH language fROIs in Experiment 2 ($t(9) = -0.579$, *n.s.*). Thus, we do not find evidence for a stronger connection between the RH language regions and the ToM network (compared to the LH language regions and the ToM network).

iv. Hierarchical clustering

The tree structures (dendrograms; Figure 7) constructed from the group-level fROI-to-fROI correlations recapitulate the hypothesis-testing results presented so far, but using a data-driven approach (in contrast to the hypothesis-driven grouping of fROIs into pre-defined networks in the previous sections). The hierarchical structure discovered in the data is dominated by the division into functional networks: in both the resting state and story comprehension conditions, the top-most partition separates out the MD fROIs from the ToM and language fROIs; one branch below, within the language-ToM cluster, segregation between language and ToM regions is mostly maintained, with the exception of the AngG language fROIs, which cluster with the ToM network (see also Blank et al., 2014, Chai et al., 2016, and Mahowald & Fedorenko, 2016, for additional evidence that the AngG language fROIs pattern differently from the rest of the language network). Hence, here too, we observed a tripartite organization into functional networks, where language and ToM fROIs are more closely related to each other than to MD fROIs. The modularity metric supports the hypothesis that the dominant organizing principle is that of functional specialization: at rest, modularity peaks at three clusters, whereas during story comprehension it peaks at two clusters, in line with the observed increase in synchronization between the language and ToM networks during story processing.

Discussion

Across three fMRI experiments we examined the relationship between three large-scale networks in humans, supporting language processing, social cognition (theory of mind, or ToM, network), and executive function (multiple demand, or MD, network). We found that the language and ToM networks show synchronized activity at rest, which further increased during story comprehension. This finding suggests a degree of functional integration between these otherwise dissociable sets of cortical regions. Importantly, the observed synchronization was selective: neither network was correlated with signal fluctuations in the domain-general MD network.

Language and Theory of Mind are deeply inter-connected aspects of human cognition, which possibly co-evolved (e.g., Hurford et al., 1998; Pinker, 2010; Malle, 2002; Woensdregt & Smith, 2017). For example, according to some evolutionary accounts, increases in social complexity led to the increase in general intelligence as well as the emergence of a robust communication system in the form of language (e.g., Dunbar & Shultz, 2007; Reader & Laland, 2002; Borrego & Gaines, 2017; Southgate, Chevallier & Cibra, 2010). This view finds support in the literature on child and adult language processing, where successful comprehension has been argued to require access to knowledge of the mental state of the conversation partner (e.g., Nadig & Sedivy, 2002; Brown-Schmidt et al., 2008; Heller et al., 2008). According to other accounts, the increasing sophistication of our communication skills has allowed for richer mental state inferences (e.g., Heyes & Frith, 2014; de Villiers & de Villiers, 2014; Astington & Baird, 2005). This view finds support in the developmental literature: acquiring certain words or constructions appears to be critical for the development of mentalizing abilities. Knowledge of mental state

verbs and sentential embedding correlate with success on false belief tasks (e.g., Dunn et al., 1991; Astington & Jenkins, 1999; de Villiers, 2000; Wellman et al., 2001; Watson et al., 2002; Astington & Baird, 2005; Milligan et al., 2007), and training children who do not pass false belief tasks on the relevant words/constructions allows them to pass those tasks (e.g., Appleton & Reddy, 1996; Slaughter & Gopnik, 1996; Clements et al., 2000; Hale & Tager-Flusberg, 2003, Lohmann & Tomasello, 2003). This causal relationship is also observed in deaf individuals born to hearing parents, who often lack linguistic input during early childhood, and who exhibit delays in ToM development (e.g., Peterson & Siegal, 2000; Wolfe et al., 2002; Schick et al., 2002; de Villiers, 2005; Schick et al., 2007; Pyers & Senghas, 2009).

In spite of this deep connection, the computational demands of language processing and mentalizing are different (cf. Sperber & Wilson, 2002; Goodman & Stuhlmuller, 2013). Language comprehension requires us to interpret linguistic signals with respect to our knowledge of meaning-form mappings, and language production requires us to select the relevant linguistic forms to convey the intended meanings (e.g., Jackendoff, 2002; Goldberg, 1995). Our linguistic knowledge is plausibly stored within the left-lateralized language network, which responds selectively during language processing (e.g., Fedorenko et al., 2011; Monti et al., 2012). In contrast, mentalizing requires us to map observed behaviors onto invisible mental states, and to predict behavior from attributed mental states (e.g., Dennett, 1978; Premack & Woodruff, 1978; Wellman, 1979, 1985). These computations appear to be supported by a bilateral network, which includes regions in the temporo-parietal junction and along the cortical midline (e.g., Fletcher et al., 1995; Gallagher et al., 2000; Saxe & Kanwisher, 2003; Saxe & Wexler, 2005). And yet, given that most linguistic exchanges concern our own or others' mental states (e.g., Dunbar, 1994; Emler, 1994; Dunbar et al., 1997; Feinberg et al., 2012), and go beyond the literal meaning

of utterances (e.g., Grice 1957, 1968, 1975; Sperber & Wilson, 1986; Benz et al., 2006; Frank & Goodman, 2012; Goodman & Frank, 2016), the language and the ToM networks must have a way to interact.

Deen et al. (2015) reported small overlap between language processing and mental state reasoning within superior temporal cortex. As Deen et al. acknowledge, neural overlap is ambiguous: it can reflect i) engagement of the relevant region in multiple cognitive processes, perhaps in a context-dependent fashion, similar to the regions of the domain-general multiple demand (MD) network (e.g., Friedman et al., 2001; Duncan et al., 2000; Duncan & Owen, 2000; Fedorenko et al., 2013; Hugdahl et al., 2015; Miyake et al., 2001; Wallis et al., 2001; Asaad et al., 2000; Mitchell et al., 2016), ii) a shared computation, or iii) some kind of integration process that combines information from multiple domains (e.g., Cole et al., 2010). More work is needed to distinguish among these interpretations. Here, we focused on another, possibly complementary, way in which the language and ToM networks could communicate: synchronization of neural fluctuations, after removing the small number of overlapping voxels (e.g., Gray & Singer, 1989; Engel et al., 2001; Fries et al., 2001; Fries, 2005; Buckner et al., 2013). We examined such fluctuations during naturalistic cognition – resting state (Experiment 1a) and story comprehension (Experiments 1b and 2) – and observed reliably synchronized activity, with higher synchronization during story comprehension. The two networks were still robustly dissociable, as evidenced by higher within-network compared to between-network correlations. Nevertheless, the inter-network synchronization is intriguing, especially given its selectivity: the language network does not synchronize with the MD network (Blank et al., 2014, replicated here in Experiments 1a-b), which has been argued to play a role in some aspects of language processing (see Fedorenko, 2014, for a review); and the ToM network similarly does

not synchronize with the MD network, despite arguments that certain ToM tasks have high executive demands (e.g., Lewis & Osborne, 1990; Roth & Leslie, 1998; Wellman et al., 2001; Carlson & Moses, 2001; Carlson et al., 2015; Rubio-Fernandez & Geurts, 2015; Powell & Carey, 2017).

What do language-ToM correlations reflect? Prior studies have suggested that functional correlations reflect anatomical connectivity and/or history of co-activation (e.g., Deco and Corbetta 2011; Deco et al., 2010, 2013; for reviews and additional accounts, see He et al., 2008; Keller et al., 2011; Matsui et al., 2011; Schölvinck et al., 2010; Shmuel & Leopold, 2008; Warren et al., 2017). Whether the inter-network correlations reported here correspond to anatomical connections remains to be discovered. The co-activation history account seems a priori plausible given that language processing and mentalizing are often engaged simultaneously in our daily life. However, it will be important in future work to characterize the *precise conditions* under which neural activity in both networks increases. One way to do so will be to further probe the degree and nature of task-dependence of the language-ToM correlations. In the current study, story comprehension elicited stronger inter-network synchronization than rest. In the future, one can systematically vary different properties of naturalistic stimuli (e.g., linguistic vs. non-linguistic, or high vs. low in mental state content) to examine the effects of those properties on the strength of language-ToM correlations. Another way to shed light on this question will be to identify the time periods in the naturalistic stimuli that show the highest inter-system correlations. These time periods can be analyzed for their linguistic/social features, and specific hypotheses can be generated about the causes for synchronization increases and subsequently tested using new materials. fMRI is not ideally suited for this approach; more temporally sensitive methods, like MEG (Baillet, 2017) or ECoG (Jacobs & Kahana, 2010), will

likely yield clearer answers.

One interesting result in the current study emerged in the analysis of LH vs. RH language regions' synchronization with the ToM system. Given the RH language system's alleged role in non-literal comprehension and pragmatic reasoning (e.g., Joanette et al., 1990; Kuperberg et al., 2000; Coulson & Williams, 2005; Mashal et al., 2005; Eviatar et al., 2006), one might expect stronger correlations between the RH language regions and the ToM regions, compared to the LH language regions and the ToM system. Yet we found that, if anything, ToM regions are more strongly correlated with the LH language fROIs in Experiment 1. One thing to keep in mind is that in many prior imaging and patient studies, it is difficult to determine whether the relevant effects arise within the RH language regions or the nearby regions of the ToM network (e.g., the rTPJ, the most selective component of the ToM network; Saxe & Powell, 2006). The latter possibility is in line with a few recent neuroimaging studies that have reported responses to non-literal phenomena like jokes and sarcasm in ToM regions, and not in the RH homologs of the language regions (e.g., Mason et al., 2008; Spotorno et al., 2012; Kline et al., in revision).

Finally, pragmatic deficits – which plausibly arise at the interface of language and social cognition – characterize numerous developmental disorders, like autism (e.g., Dewey & Everard, 1974; Tager-Flusberg, 1981; Baron-Cohen, 1988; Happé, 1993; Baron-Cohen et al., 1997) or Social Communication Disorder (e.g., Swineford et al., 2014), and commonly arise in individuals with acquired brain damage (e.g., Joanette et al., 1990; Kaplan et al., 1990; McDonald, 1992, 1993; Boone & Plante, 1993; Ozonoff & Miller, 1996; Pearce et al., 1998; Docking et al., 2000; Harciarek & Jodzio, 2005; Kertesz et al., 2007). The current findings might provide a potential neural marker of successful language-ToM system interaction, and future studies could examine potential deviations from the observed pattern in individuals with pragmatic difficulties or in

typical development. Relatedly, inter-individual variability in the strength of the language-ToM correlations among neurotypical adults can in the future be related to behavioral variability in pragmatic abilities.

To conclude, we observed significant synchronization of neural fluctuations between the language and ToM networks, which was especially strong during story comprehension. This synchronization may support successful communication, which requires language and social reasoning to work in concert.

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1076

1077 Table 1

1078 *Timing parameters for the different versions of the language localizer task.*

1079

	Version			
	A	B	C	D
Number of participants	16	4	4	2
Task: Passive Reading or Memory?	PR	M	M	M
Words / nonwords per trial	12	8	12	12
Trial duration (ms)	6,000	4,800	6000	6000
Fixation	100	300	300	300
Presentation of each word / nonword	450	350	350	350
Fixation	500	---	---	---
Memory probe	---	1350	1000	1000
Fixation	---	350	500	500
Trials per block	3	5	3	3
Block duration (s)	18	24	18	18
Blocks per condition (per run)	8	4	6	8
Conditions	Sentences Nonwords	Sentences Nonwords Word-lists*	Sentences Nonwords Word-lists*	Sentences Nonwords
Fixation block duration (s)	14	16	18	18
Number of fixation blocks	5	3	4	5
Total run time (s)	358	336	396	378
Number of runs	2	3-4	2-3	2

1080 * Used for the purposes of another experiment; see (Fedorenko et al., 2010).

1081
 1082 Table 2
 1083 *Excerpts from three of the stories in the story comprehension task. In bold we marked a few*
 1084 *examples of mental state content.*

1085

Examples	
The Bradford Boar	[...] ...the people of Bradford had second thoughts about visiting the well. That the people of Bradford bore the brunt of the beast's ferocity was unfair in the eyes of the people of the region. [...] By the handsome reward many felt tempted... [...] Seeing the slain carcass of the boar the huntsman rejoiced in his good fortune. [...] He was suddenly realizing his tricky situation could end badly for him. [...] Listening to the tale, the Lord of the Manor tried to discern which huntsman was telling him the truth. [...]
King of Birds	[...] The eagle, who already thought himself the de facto king, arrived fashionably late. It was a hawk who was most excited about the meeting... [...] It was decided that the bird that could fly the highest should be king. [...] The little bird lay low near the eagle at first, but the eagle did not notice the bird hopping onto his back... [...] ... and he laughed to himself at how easy it had been to outwit the other birds. [...]
Elvis	[...] ... I could not figure out what this Elvis Presley guy had that the rest of us boys did not have. [...] When I got my new Buster Brown shoes, I was smiling from ear to ear . [...] I cried desperately . [...] ... from his expression I could tell that he wished he could cut it as I had asked. [...] "I am not a baby", I said as I wiped the tears from my eyes . [...] My head was no longer in the clouds . [...]

1086

Table 3

Within-network correlations per hemisphere and between hemispheres. Correlations are highly significant ($p < 10^{-7}$) within each of the three networks, both at rest and during story comprehension. The language and MD correlations replicate Blank et al., 2014. The within ToM correlation is robust too, as shown by the replication results.

Experiment	Hemisphere	Language	ToM	MD
1a. Rest	LH	0.49 (0.19)	0.54 (0.15)	0.46 (0.17)
	RH	0.37 (0.14)	0.57 (0.21)	0.46 (0.17)
	LH-RH	0.26 (0.15)	0.41 (0.17)	0.3 (0.15)
1b. Stories	LH	0.69 (0.17)	0.59 (0.13)	0.48 (0.14)
	RH	0.45 (0.15)	0.58 (0.16)	0.48 (0.14)
	LH-RH	0.43 (0.13)	0.49 (0.13)	0.38 (0.11)
2. Stories Replication	LH	0.67 (0.19)	0.45 (0.09)	
	RH	0.43 (0.14)	0.51 (0.08)	
	LH-RH	0.39 (0.11)	0.41 (0.07)	

Figure Captions

Figure 1. Sample trials from the functional localizer paradigms. **Language:** sentences were contrasted with sequences of pronounceable non-words. **ToM:** vignettes about false mental states were contrasted with vignettes about false physical states, each followed by a true/false statement. **MD:** Harder and easier versions of a spatial working memory task (location memory) were contrasted, each followed by a two-alternative forced choice question and feedback.

Figure 2. Masks used to constrain the selection of subject-specific voxels for each functional region of interest in the three networks. **Language** (red): 1. *LIFGorb*, inferior frontal gyrus, orbital portion, 2. *LIFG*, 3. *LMFG*, left middle frontal gyrus, 4. *LAntTemp*, left anterior temporal cortex; 5. *LPostTemp*, left posterior temporal cortex; 6. *LAngG*, left angular gyrus. **ToM** (green): 1. *TPJ*, temporo-parietal junction; 2. *DMPFC*, dorsal medial prefrontal cortex; 3. *MMPFC*, middle medial prefrontal cortex; 4. *VMPFC*, ventral medial prefrontal cortex; 5. *PC*, posterior cingulate cortex and precuneus; **MD** (blue): 1. *IFGop*, opercular IFG; 2. *MFG* and 3. *MFGorb*, middle frontal gyrus and its orbital portion; 4. *PrecG*, precentral gyrus; 5. *Insula*; 6. *SMA*, supplementary motor area; 7. *ParInf*, inferior parietal cortex; 8. *ParSup*, superior parietal cortex; 9. *ACC*, anterior cingulate cortex.

Figure 3. Responses of each network's fROIs to its localizer conditions. Bars correspond to percent signal change, relative to rest, in response to the target and control conditions of each localizer. The difference between each pair of bars is the size of the localizer contrast effect, which was the basis for fROI definition. The responses shown were estimated with two-fold across-runs cross-validation, so that the data used for response estimation were independent from

data used for fROI definition.

Figure 4. Matrices for fROI-to-fROI correlations. The three columns correspond to Experiments 1a (resting state), 1b (stories), and 2 (stories replication; NB: MD fROIs were not defined in that experiment). The top row shows all correlations, the bottom row highlights the significant ones (at $p < 0.05$, false discovery rate (FDR) corrected), with the non-significant ones colored in black. The order of the fROIs across rows and columns corresponds to the numbers used in Figure 2; within each network, the regions are sorted by hemisphere (LH, left hemisphere; RH, right hemisphere). Qualitatively, these matrices illustrate our key findings: each of the three network is internally integrated; the language and ToM network are further synchronized, especially during story comprehension, albeit dissociable. The language and ToM networks are not correlated with the MD system.

Figure 5. Average within- and between-network correlations for Experiment 1a, resting state (top), Experiment 1b, story comprehension (middle), and Experiment 2, story comprehension replication (bottom). Error bars are standard errors of the mean by participants. Grey circles correspond to the individual participants' values. Vertical curves are Gaussian fits to empirical null distributions. Significant correlations (Bonferroni-corrected within each experiment; see Methods) are marked with asterisks.

Figure 6. Comparison of between-network correlations for LH language regions and the ToM network (bright yellow) vs. RH language regions and the ToM network (pale yellow). The bright red and green bars show the same data as shown in Figure 4. The pale red bar shows the average

within-system correlation for the RH language fROIs. Error bars are standard errors of the mean by participants. Grey circles correspond to the individual participants' values. Vertical curves are Gaussian fits to empirical null distributions. The hypothesis that RH language regions play a special role in pragmatic, ToM-based inference predicts stronger correlations between RH language regions and the ToM network (compared to the LH language regions and the ToM network). This prediction was not supported in any of our experiments.

Figure 7. Results of hierarchical clustering for Experiment 1a, resting state (left) and Experiment 1b, story comprehension (right). Hierarchical clustering creates a binary tree where branch length (horizontal lines) corresponds to the similarity (here, average correlation across participants) between fROIs. The color of the dots on the y-axis represents our *a priori* assignment of fROIs to networks: MD (blue), language (red), and ToM (green). Above each tree diagram, modularity is plotted for all fROI partitions in the tree. Each point in the modularity plot corresponds to a partition: an imaginary vertical line drawn from a location where two fROIs or clusters of fROIs connect to form a higher-level cluster. The dashed lines represent the points of maximum modularity, which correspond to a partition into networks. During resting state, maximum modularity is at a partition into 3 clusters: MD (blue lines), language (red lines), and ToM (green lines). All fROIs are correctly assigned to clusters, apart from the bilateral angular gyri (AngG) which are assigned to the ToM cluster despite being defined with the language localizer. During story comprehension, maximum modularity is at a two-partite division: an MD cluster (blue) and a language-ToM cluster (yellow). Within the latter, fROIs mostly remain segregated into language and ToM fROIs, except for the left angular gyrus (LH-AngG).

1163 *Figure 8.* A representation of the same data as in Figure 4, with individual data points color-
1164 coded for participants' sex: red – female, blue – male. Despite the smaller number of males in
1165 our samples, the observed pattern of correlations is similar for males and females.

1166

Language

Sentences

+	THE	SPEECH ...	WAS	TOO	LONG	FOR	THE	MEETING	+
---	-----	------------	-----	-----	------	-----	-----	---------	---

Non-words

+	LAS	TUPING ...	CRE	POME	VILLPA	OLP	PRONT	CHO	+
100ms	450ms	450ms	450ms	450ms	450ms	450ms	450ms	450ms	500ms

Theory of Mind

False Belief

+	The morning of the high school dance Sarah placed her high heel shoes under her dress and then went shopping. That afternoon, her sister borrowed the shoes and later put them under Sarah's bed.	Sarah gets ready assuming her shoes are under the dress. True False	+
---	---	---	---

False Physical

+	A large oak tree stood in front of City Hall from the time the building was built. Last year the tree fell down and was replaced by a stone fountain.	An antique drawing of City Hall shows a fountain in front. True False	+
12s	12s	4s Response	12s

Multiple Demand

Easy

+								+
---	--	--	--	--	--	--	--	---

Hard

+								+
500ms	1000ms	1000ms	1000ms	1000ms	3000ms	Response	250ms Feedback	3500ms

A. Language

B. Theory of Mind

C. Multiple Demand

Expt 1a: Rest

 $n = 15$

Fisher-transformed correlations

Expt 1b: Stories

 $n = 16$

*

Expt 2: Stories replication

 $n = 10$ Within LH
languageWithin RH
LanguageLH Language-
ToMRH Language-
ToMWithin
ToM

Expt 1a. Rest

Expt 1b. Stories