Differential tracking of linguistic vs. mental state content in naturalistic stimuli by language and Theory of Mind (ToM) brain networks

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Contributions

AP, IB and EF developed the concept for the study. AP, IB and JG selected / created experimental materials. AP, IB, OJ and ZM collected and analyzed the data. AP performed the final version of the statistical analyses for the current study that are reported here. AP, IB, and EF wrote the manuscript with input from other co-authors.

Conflict of interest

Authors report no conflict of interest.

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Short title: Language vs. ToM Networks in Naturalistic Stimulus Tracking

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Abstract

Language and social cognition, especially the ability to reason about mental states, known as Theory of Mind (ToM), are deeply related in development and everyday use. However, whether these cognitive faculties rely on distinct, overlapping, or the same mechanisms remains debated. Some evidence suggests that, by adulthood, language and ToM draw on largely distinct—though plausibly interacting—cortical networks. However, the broad topography of these networks is similar, and some have emphasized the importance of social content / communicative intent in the linguistic signal for eliciting responses in the language areas. Here, we combine the power of individual-subjects functional localization with the naturalistic-cognition inter-subject correlation approach to illuminate the language-ToM relationship. Using fMRI, we recorded neural activity as participants (n=43) listened to stories and dialogs with mental state content (+linguistic, +ToM), viewed silent animations and live action films with mental state content but no language (-linguistic, +ToM), or listened to an expository text (+linguistic, -ToM). The ToM network robustly tracked stimuli rich in mental state information regardless of whether mental states were conveyed linguistically or non-linguistically, while tracking a +linguistic/-ToM stimulus only weakly. In contrast, the language network tracked linguistic stimuli more strongly than a) non-linguistic stimuli, and than b) the ToM network, and showed reliable tracking even for the linguistic condition devoid of mental state content. These findings suggest that in spite of their indisputably close links, language and ToM dissociate robustly in their neural substrates, and thus plausibly cognitive mechanisms, including during the processing of rich naturalistic materials.

1. Introduction

Language and social cognition, especially the ability to reason about mental states, known as Theory of Mind or ToM, are deeply related in human development, everyday use, and possibly evolution. After all, language use is a communicative behavior, which is a kind of cooperative behavior, and cooperative behaviors are, in turn, a kind of social behavior (e.g., Grice, 1968, 1975, Sperber & Wilson, 1986). Construed this way, language can hardly be encapsulated from social cognition (cf. Fodor, 1983); it is subsumed *within* social cognition. Interpreting linguistic signals bears key parallels to the interpretation of other intentional behaviors (e.g., Grice, 1975; Sperber & Wilson, 1986). Communicative utterances, like other behaviors, are assumed to have goals, and conversation partners are assumed to pursue these goals rationally. Furthermore, everyday discourse appears to be dominated by information about other people (e.g., Dunbar, Marriott & Duncan, 1997), and the need to keep track of others' social record has been proposed as a key driver of language evolution (e.g., Dunbar, 2004; Nowak & Sigmund, 2005; Sommerfield, Krambeck & Milinski, 2008; Nowak & Highfield, 2011). Lastly, evidence of others' mental states conveyed through language is arguably richer and certainly more direct / less ambiguous than what can be inferred from non-linguistic intentional behavior alone: trying to infer the beliefs guiding someone's actions can be obviated by their telling you what those beliefs are.

Yet in the relatively brief history of cognitive neuroscience, the study of language and of social cognition have, for the most part, proceeded independently. The two cognitive domains have been treated, often implicitly, as components of a "nearly decomposable system" (Simon, 1962)

– a system in which interactions between the component subsystems (language and social cognition here) are sufficiently less common than interactions among each subsystem's parts to warrant a "divide and conquer" strategy (Saxe, Brett, & Kanwisher, 2006). On such a strategy, each subsystem can first be investigated on its own, leaving questions of potential dependencies between subsystems for a later stage. The application of this strategy to language and social cognition has been remarkably successful, and even this later stage is now coming within reach. But is near-decomposability a true property of the relationship between language and social cognition, or merely a simplifying assumption? It is difficult to say because most studies to date have deliberately aimed to isolate one or the other component subsystem rather than probe their relationship (cf. Deen et al., 2015; Paunov et al., 2019; Braga et al., 2020). So we know that language and social cognition *can* dissociate, under appropriate experimental conditions. But do they, in fact, dissociate in everyday, naturalistic cognition? This is the question we tackle in the current study.

Before we proceed to describe the current study, we review what is currently known about the neural bases of linguistic processing and of Theory of Mind.

Language network. Language processing engages a network of left-lateralized brain regions in lateral frontal and temporal cortex. These regions support lexico-semantic processing (word meanings) and combinatorial morpho-syntactic and semantic processing (e.g., Fedorenko et al., 2010, 2012, 2016, 2020; Bautista & Wilson, 2016; Blank et al., 2016; Anderson et al., 2018; Reddy & Wehbe, 2020). Responses to linguistic stimuli generalize across different materials, tasks, modalities of presentation (reading vs. listening), languages, and developmental trajectories (e.g., Fedorenko et al., 2010; Bedny et al., 2011; Fedorenko, 2014; Scott et al., 2017; Diachek, Blank, Siegelman et al., 2020; Ayyash, Malik-Moraleda et al., in prep.; Ivanova et al., in prep.). In contrast to these robust and consistent responses to linguistic stimuli, these regions do not respond to a wide range of non-linguistic cognitive processes, including arithmetic processing, music perception, executive function tasks, action or gesture observation, non-verbal social-cognitive tasks, and the processing of computer code (e.g., Fedorenko et al., 2011; Monti et al., 2012; Pritchett et al., 2018; Almaric & Dehaene, 2018; Paunov, 2019; Jouravlev et al., 2019; Ivanova et al., 2020; Shain, Paunov et al., in prep.; see Fedorenko & Varley, 2016 for a review).

ToM network. Attribution of mental states, such as beliefs, desires, and intentions, engages a network of brain regions in bilateral temporo-parietal cortex and anterior and posterior regions along the cortical midline. These responses generalize across the type of mental state, its specific content or format (linguistic vs. pictorial), and the source of evidence for it (e.g., Fletcher et al., 1995; Castelli et al., 2000; Gallagher et al., 2000; Vogeley et al., 2001; Ruby & Decety, 2003; Saxe & Kanwisher, 2003; Saxe, Schulz, & Jiang, 2006; Jacoby et al., 2016; see Koster-Hale & Saxe, 2013 for review) as well as across populations with diverse cultural backgrounds or developmental experiences (e.g., Callaghan et al., 2005; Sabbagh et al., 2006; Shahaeian et al., 2011; Koster-Hale, Bedny, & Saxe, 2014; Richardson et al., 2018, 2020). However, by adulthood, these regions, and especially the most selective component of the ToM network, the right temporo-parietal junction (RTPJ), do not respond to social stimuli, like faces, voices, or biological motion (e.g., Deen et al., 2015), to general executive demands (e.g., Saxe, Schulz, & Jiang, 2006), to physical or broadly social attributes of agents, or to attribution of bodily sensations of pain and hunger (e.g., Saxe & Powell, 2006; Bruneau, Pluta & Saxe, 2012; Jacoby et al., 2016).

Together, these two lines of work support the notion that language and ToM are ‘natural kinds’—distinct cognitive faculties that carve human nature at the joints—each one mapping onto functionally specialized neural structures. Investigations of developmental and acquired disorders have provided convergent support for the dissociability of language and ToM. Individuals with even severe aphasia appear to retain the capacity for mental state reasoning as long as non-verbal materials are used (e.g., Varley & Siegal, 2000; Varley, Siegal & Want, 2001; Apperly et al., 2006; Willems et al., 2011; see Fedorenko & Varley, 2016 for review). And at least some individuals with social, ToM-related impairments (e.g., individuals with autism spectrum disorders) show preservation of lexical and syntactic linguistic abilities (e.g., Frith & Happe, 1994; Wilkinson, 1998; Tager-Flusberg, Paul & Lord, 2005; Tager-Flusberg, 2006). But as noted above, most of this evidence has come from traditional, task-based experimental paradigms, and such paradigms are well-suited to the divide-and-conquer enterprise, but may overestimate the degree of separation. Indeed, Paunov et al. (2019) recently examined inter-regional functional correlations within and between the language and ToM networks during naturalistic cognition paradigms, like story comprehension, and found that in spite of their dissociability (stronger within- than between-network correlations), the language and ToM networks also showed a significant amount of synchronization in their neural activity. These results point to some degree of functional integration between the networks. Furthermore, several prior studies have argued for the importance of social content / communicative intent in the linguistic signal for eliciting responses in the language areas (e.g., Mellem et al., 2016; Redcay et al., 2016). Here, we adopt an approach that relies on the use of rich naturalistic stimuli but allows us to not only examine the structure of and the relationship between the networks, but to also ask what stimulus features each network "tracks" through the inter-subject correlation approach (e.g., Hasson et al., 2004, 2008).

2. Materials and Methods

2.1. General approach.

Following Blank & Fedorenko (2017, 2020), we combine two powerful methodologies, which have previously been productively applied separately in the domains of language and social cognition. In particular, we use *functional localization* (e.g., Brett et al., 2002; Saxe et al., 2006; Fedorenko et al., 2010) to identify the two networks of interest in individual subjects, and *inter-subject correlations* (ISCs; e.g., Hasson et al., 2004, 2008) to examine the degree to which these networks track different stimulus features during the processing of rich naturalistic materials. Here, we highlight key strengths of each approach and consider their synergistic advantages given our current goals.

Naturalistic paradigms have become a crucial complement to traditional, task-based studies in cognitive neuroscience. The obvious advantage of naturalistic paradigms is their high ecological validity: by giving up a measure of experimental control, it becomes possible to study cognition "in the wild" (Blank & Fedorenko, 2017; see e.g., Sonsukare et al., 2019 and Nastase et al., 2020 for general discussions). In particular, one can examine how coherent and structured mental representations are extracted from rich and noisy perceptual inputs, which is what happens in everyday cognition. This is in contrast to trying to artificially isolate various features of these perceptual inputs, as is typically done in constrained experimental tasks. Naturalistic paradigms have been argued to elicit more reliable responses compared to traditional, task-based paradigms (Hasson et al., 2010), perhaps because they are generally more engaging, and can enable discoveries of functional relationships among brain regions and networks that are altogether missed in more constrained settings (e.g., Gallivan, Cavina-Pratesi & Culham, 2009). Another advantage of naturalistic paradigms is their hypothesis-free nature. Through the use of naturalistic materials, researchers impose minimal design constraints to investigate the domain of interest in a manner that is maximally unbiased by prior theoretical assumptions. In effect, they are letting the data speak for itself.

However, naturalistic paradigms also come with an inherent analytic challenge: how do we make sense of data acquired without the typical constraints of standard hypothesis-driven modeling approaches? Hasson et al. (2004) pioneered an approach to tackle this challenge, known as the inter-subject correlation (ISC) approach (see Hasson et al., 2008, for an overview), which we adopt in the current study. The key insight behind the ISC approach is that we can model any given participant’s fMRI signal time series using another participant’s or other participants’ time series: if a voxel, brain region, or brain network ‘tracks’ features of the stimulus during which the time series were obtained, then fMRI signal fluctuations will be stimulus-locked, resulting in similar time courses across participants (i.e., high inter-subject correlations).

ISCs have been used in several studies of narrative comprehension (e.g., Wilson et al., 2007; Lerner et al., 2011; Honey et al., 2012; Regev et al, 2013; Silber et al., 2014; Schmälzle et al., 2015; Blank & Fedorenko, 2017, 2020), and whole-brain voxel-wise analyses have revealed high inter-subject correlations across large swaths of cortex that resemble the union of the language and ToM networks. On their own, these results might be taken as *prima facie* evidence for non-dissociability of language and ToM, given that the two networks appear to be jointly recruited. And insofar as the mental processes recruited in narrative comprehension recapitulate those used in everyday abstract cognition—an assumption that, we take it, partially justifies the interest in narratives in cognitive science and neuroscience (e.g., Finlayson & Winston, 2011; Willems et al., 2020)—the results may be taken to suggest the non-dissociability of language and ToM more generally.

However, it is difficult to draw inferences from these studies about the *relative* contributions of the language and ToM networks to narrative comprehension for two reasons. First, in whole-brain analyses, ISCs are computed on a voxel-wise basis: individual brains are normalized to a stereotaxic template, and one-to-one voxel correspondence across individuals is then assumed in computing the ISCs. This is problematic because i) inter-individual variability is well established in the high-level association cortex (e.g., Fischl et al., 2008; Frost & Goebel, 2012; Tahmasebi et al., 2012), so any given voxel may belong to functionally distinct regions across participants; and ii) there is no independent criterion based on which an anatomical location can be interpreted as belonging to the language vs. the ToM network, thus necessitating reliance on the fallacious “reverse inference” (Poldrack, 2006) to interpret the resulting topography (see Fedorenko, 2021, for discussion). And second, traditional whole-brain analyses typically include all voxels that showed significant (above baseline) ISCs, thus potentially obscuring large differences in effect sizes (cf. Blank & Fedorenko, 2017; see Chen, Taylor & Cox, 2017, for a general discussion of the importance of considering effect sizes in interpreting fMRI findings). Combining the ISC approach with individual-participant functional localization enables us to identify and directly compare the networks of interest (including with respect to effect sizes), as well as to relate the findings straightforwardly to the prior literature on the language and ToM networks. In the current study, we therefore identified the language and ToM networks using well-established functional localizers (Saxe & Kanwisher, 2003; Fedorenko et al., 2010), and then examined the degree of inter-subject synchronization in those regions during the processing of diverse naturalistic linguistic and non-linguistic conditions varying in the presence of mental state content. If the language and ToM networks are dissociable during naturalistic cognition, we would expect the language regions to track linguistic stimuli, including those that lack mental state content, and the ToM regions to track stimuli that have mental state content, including both linguistic and non-linguistic ones.

2.2. Experimental design and statistical analyses

Our overall design and analytic strategy were as follows: participant-specific regions that responded more strongly during the reading of sentences compared with lists of nonwords were defined as regions of interest comprising the language network. Similarly, regions that responded more strongly to stories about others' beliefs vs. stories about physical reality were defined as regions of interest comprising the ToM network. Whereas the precise anatomical locations of these regions were allowed to vary across participants, their overall topography was constrained by independently derived criteria to establish functional correspondence across brain regions of different participants (e.g., Fedorenko et al., 2010; Julian et al., 2012).

Activity in these two sets of brain regions was recorded with fMRI while participants listened to or watched a series of naturalistic stimuli, as detailed below. For each region in each network, our critical dependent variable was the strength of the correlation between each participant's time series and the average time series from the rest of the participants. The group-averaged ISC in each region was tested for significance via a permutation test of the time series data. For our critical analysis, all individual ISC values were modeled using a linear mixed-effects regression with participant, brain region, and stimulus (what we call 'condition' below) as random effects.

2.3. Participants

Forty-seven native English speakers (age 19-48, $M = 24.5$, $SD = 5.08$; 30 female) from MIT and the surrounding Boston community participated for payment. Forty participants were right-handed, as determined by the Edinburgh handedness inventory (Oldfield 1971) or by self-report (n=1). All seven left-handed participants showed typical left lateralization in the language localizer task described below (see Willems et al., 2014, for arguments to include left handers in cognitive neuroscience research). Four participants were excluded from the analyses due to poor quality of the localizer data (2 for ToM localizer, 1 for language localizer, and 1 for both), with the exclusion criterion defined as fewer than 100 suprathreshold voxels (at the $p < 0.001$ uncorrected whole-brain threshold) across the respective network's masks (see below), bringing the number of participants included in the critical analyses to 43. All participants gave informed consent in accordance with the requirements of MIT's Committee on the Use of Humans as Experimental Subjects (COUHES).

2.4. Stimuli and procedure

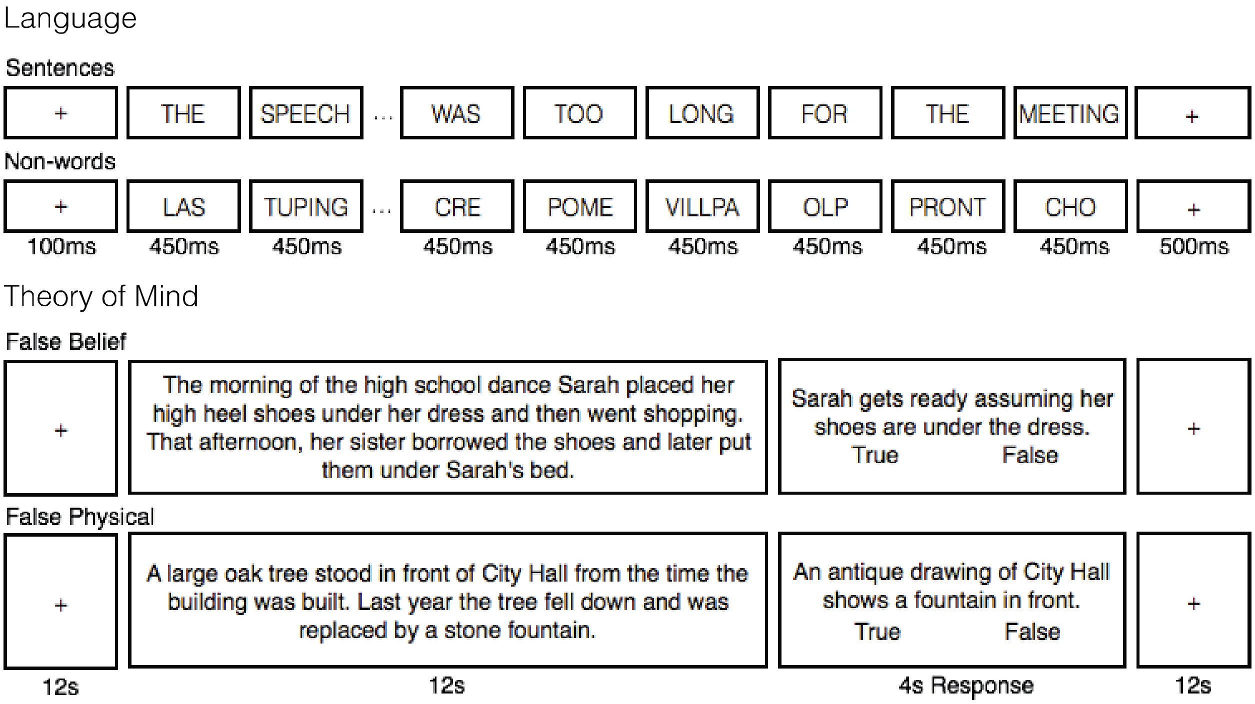
Each participant completed a language localizer, a ToM localizer, a localizer for the domain-general Multiple Demand (MD) system (used in a replication analysis, as described below), and a subset, or all, of the critical naturalistic stimuli ('conditions') (between 1 and 7) due to scan duration constraints (18 participants completed all 7 conditions of interest, 1 participant completed 6 conditions, 10 participants completed 5 conditions, 1 participant completed 4 conditions, 1 participant completed 3 conditions, 7 participants completed 2 conditions, and 5 participants completed 1 condition). Each condition was presented to between 28 and 32 participants (see **Table 1**). Each stimulus, lasting ~5-7 minutes (see **Table 1** for precise durations), was preceded and followed by 16 s of fixation. Finally, ten participants performed a resting state scan, used in one of the reality-check analyses, as described below. For the language localizer, 36/43 participants completed it in the same session as the critical conditions, the remaining 7 participants completed it in an earlier session. Similarly, for the ToM and MD localizers, 37/43 participants completed them in the same session as the critical conditions, the remaining 6 participants completed them in an earlier session.

Condition	**Duration**	**N**
+Lang +ToM		
Story	5m 16s	31
Audio play	6m 14s	29
Dialog	5m 35s	28
-Lang +ToM		
Animated short film	5m 48s	32
Live action movie clip	6m 10s	30
Intentional shapes animation	4m 50s	30
+Lang -ToM		
Expository text	7m 6s	28
-Lang -ToM (control)		
Resting state	5m 0s	10

Table 1. *Naturalistic conditions in each of the three conditions types of interest and reality-check (resting state), including durations, and number of participants per condition. Durations include 16 s fixations at the beginning and end of the scan (32 s total).*

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. Briefly, we used a reading task contrasting sentences and lists of unconnected, pronounceable nonwords (**Figure 1**) in a blocked design with a counterbalanced condition order across runs. Stimuli were presented one word / nonword at a time. Participants read the materials passively (we included a button-pressing task at the end of each trial, to help participants remain alert). As discussed in the introduction, this localizer is robust to task manipulations (e.g., Fedorenko et al., 2010; Scott et al., 2017; Ivanova et al., in prep.). Moreover, this localizer identifies the same regions that are localized with a broader contrast, between listening to natural speech and its acoustically-degraded version (Scott et al., 2017; Ayyash, Malik-Moraleda et al., in prep.). All participants completed two runs, each lasting 358 s and consisting of 8 blocks per condition and 5 fixation blocks. (A version of this localizer is available from http://evlab.mit.edu/funcloc/.)

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 classic false belief paradigm (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 linguistically matched vignettes about false physical states (physical representations depicting outdated scenes, e.g., a photograph showing an object that has since been removed; the control condition) (**Figure 1**) in a long-event-related design with a counterbalanced order across runs (when multiple runs were administered). Stimuli were presented one at a time. Participants read these vignettes and answered a true / false comprehension question after each one. Forty-one participants completed two runs and two completed one run due to time limitations, each lasting 262 s and consisting of 5 vignettes per condition. (A version of this localizer is available from http://saxelab.mit.edu/use-our-efficient-false-belief-localizer.)



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

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

Figure 1. *Sample trials from the functional localizer paradigms.* ***Language****: reading of sentences was contrasted with reading of sequences of pronounceable non-words (Fedorenko et al., 2010).* ***ToM****: reading of vignettes about false mental states was contrasted with reading of vignettes about false physical states, each followed by a true/false statement (Saxe & Kanwisher, 2003).*

Multiple Demand (MD) localizer task (used in a replication analysis, as described below). The task used to localize the MD network is described in detail in Fedorenko et al. (2011) and targets brain regions that support goal-directed effortful behaviors (e.g., Duncan, 2010, 2013). Briefly, we used a spatial working-memory task contrasting a harder version with an easier version (**Supplemental Figure A1**) in a blocked design with a counterbalanced condition order across runs (when multiple runs were administered). On each trial, participants saw a 3x4 grid and kept track of eight (hard version) or four (easy version) randomly generated 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, and received feedback. Of the thirty-two participants included in the replication analysis (i.e., non-overlapping with those used in the original study in Blank & Fedorenko, 2017), twenty-three participants completed two runs of the localizer, and nine completed one run, each lasting 448 s and consisting of 6 blocks per condition and 4 fixation blocks.

The critical naturalistic task. In the main experiment, each participant listened to (over scanner-safe Sensimetrics headphones) and/or watched a set of naturalistic stimuli (varying between 4 min 50 s and 7 min 6 s in duration). Four of the conditions used linguistic materials: i) a story

("Elvis" from the Natural Stories corpus; Futrell et al., 2020), ii) an audio play (a segment from an HBO miniseries, "Angels in America", from Chapter 1: "Bad News", https://www.imdb.com/title/tt0318997/, audio only), iii) a naturalistic dialog—a casual unscripted conversation between two female friends (recorded by JG), and iv) a non-narrative expository text (a text about trees adapted from Wikipedia; https://en.wikipedia.org/wiki/Tree) (recorded by JG). The first three of the linguistic conditions were rich in mental state content; the fourth was meaningful naturalistic discourse with little/no mental state content. The three remaining conditions were videos with no linguistic content: i) an animated short film ("Partly Cloudy" by Pixar), ii) a clip from a live action film ("Mr. Bean", https://www.youtube.com/watch?v=bh__g-ZZ6WA), and iii) a custom-created Heider and Simmel style animation (Heider & Simmel, 1944) consisting of simple geometric shapes moving in ways as to suggest intentional interactions designed to tell a story (e.g., a shape gets locked up inside a space, another shape goes on a quest to get help to release it, etc.). All three non-linguistic conditions were rich in mental state content. (Five additional conditions—included in some participants for another study—are of no interest to the current study.) All the materials will be made available on OSF (except in cases where copyright issues will prevent us from doing so). In the resting state scan, used for one of our reality-check analyses, as described below, 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 projector was turned off).

2.5. Data acquisition and preprocessing

Data acquisition. Whole-brain structural and functional data were collected on a whole-body 3 Tesla Siemens Trio scanner with a 32-channel head coil at the Athinoula A. Martinos Imaging Center at the McGovern Institute for Brain Research at MIT. T1-weighted structural images were collected in 176 axial slices with 1 mm isotropic voxels [repetition time (TR) = 2530 ms; echo time (TE) = 3.48 ms]. Functional, blood oxygenation level-dependent (BOLD) data were acquired using an EPI sequence with a 90° flip angle and using GRAPPA with an acceleration factor of 2; the following parameters were used: thirty-one 4-mm-thick near-axial slices acquired in an interleaved order (with 10% distance factor), with an in-plane resolution of 2.1 x 2.1 mm, FoV in the phase encoding (A >> P) direction 200 mm and matrix size 96 x 96 mm, TR = 2000 ms and TE = 30 ms. The first 10 s of each run were excluded to allow for steady-state magnetization.

Spatial preprocessing. Data preprocessing was performed with SPM12 (using default parameters, unless specified otherwise) and supporting, custom scripts in MATLAB. Preprocessing of anatomical data included normalization into a common space [Montreal Neurological Institute (MNI) template], resampling into 2 mm isotropic voxels, and segmentation into probabilistic maps of the gray matter, white matter (WM), and cerebro-spinal fluid (CSF). Preprocessing of functional data included motion correction (realignment to the mean image using second-degree b-spline interpolation), normalization (estimated for the mean image using trilinear interpolation), resampling into 2 mm isotropic voxels, smoothing with a 4 mm FWHM Gaussian filter and high-pass filtering at 200 s.

Temporal preprocessing. Additional preprocessing of data from the story comprehension runs was performed using the CONN toolbox (Whitfield-Gabrieli and Nieto-Castañón, 2012; http://www.nitrc.org/projects/conn) 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, the residual signal was bandpass filtered (0.01 – 0.1 Hz) to preserve only low-frequency signal fluctuations (Cordes et al., 2001). This filtering did not influence the results reported below.

2.6. Participant-specific functional localization of the language and ToM (and MD, for a replication analysis) networks

Modeling localizer data. For each localizer task, a standard mass univariate analysis was performed in SPM12 whereby a general linear model estimated the effect size of each condition in each experimental run. These effects were each modeled with a boxcar function (representing entire blocks) convolved with the canonical hemodynamic response function. 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 weights were then used to compute the functional contrast of interest: for the language localizer, sentences > nonwords, for the ToM localizer false belief > false photo, and for the MD localizer (replication analysis; see Stimuli and Procedure), hard > easy spatial working memory.

Defining fROIs. Language and ToM (and MD, in the replication analysis) functional regions-of-interest (fROIs) were defined individually for each participant based on functional contrast maps from the localizer experiments (a toolbox for this procedure is available online; https://evlab.mit.edu/funcloc/). These maps were first restricted to include only gray matter voxels by excluding voxels that were more likely to belong to either the WM or the CSF based on SPM's probabilistic segmentation of the participant's structural data.

Then, fROIs in the language network were defined using group-constrained, participant-specific localization (Fedorenko et al., 2010). For each participant, the map of the sentences > nonwords contrast was intersected with binary masks that constrained the participant-specific language network to fall within areas where activations for this contrast are relatively likely across the population. These masks are based on a group-level representation of the contrast obtained from a previous sample. We used five such masks in the left-hemisphere, including regions in the mid-to-posterior and anterior temporal lobe, as well as in the middle frontal gyrus, the inferior frontal gyrus, and its orbital part (**Figure 3**). A version of these masks is available online (https://evlab.mit.edu/funcloc/). In each of the resulting 5 masks, a participant-specific language fROI was defined as the top 10% of voxels with the highest contrast values. This top *n*% approach ensures that fROIs can be defined in every participant and that their sizes are the same across participants, allowing for generalizable results (Nieto-Castañon and Fedorenko, 2012).

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 included regions in the left and right temporo-parietal junction (L/RTPJ), precuneus /

posterior cingulate cortex (L/RPC), and dorsal medial prefrontal cortex (**Figure 3**). A version of these masks is available online (available for download from http://saxelab.mit.edu/use-our-theory-mind-group-maps), but the masks were edited as follows: the RSTS (right superior temporal sulcus) mask was excluded, as it covers the entire STS, which is known to show complex functional organization, with reduced ToM selectivity (Deen et al., 2015). The middle- and ventral-medial prefrontal cortex (MMPFC and VMPFC) masks were also excluded to reduce the number of statistical comparisons in per-fROI analyses, but the dorsal MPFC and PC masks were split into left- and right-hemispheres, for a total of 6 masks.

Additionally, for the replication analysis, fROIs in the MD network were defined based on the hard > easy contrast in the spatial working memory task. Here, instead of using binary masks based on group-level functional data, we used anatomical masks (Tzourio-Mazoyer et al., 2002; Fedorenko et al., 2013; Blank et al., 2014; Blank & Fedorenko, 2017). Nine masks were used in each hemisphere, including regions in the middle frontal gyrus and its orbital part, the opercular part of the inferior frontal gyrus, the precentral gyrus, the superior and inferior parts of the parietal lobe, the insula, the supplementary motor area, and the cingulate cortex (**Supplemental Figure A2**). (We note that functional masks derived for the MD network based on 197 participants were largely overlapping with the anatomical masks; we chose to use the anatomical masks to maintain comparability between our functional data and data from previous studies that have used these masks.)

In line with prior studies (e.g., Blank, Fedorenko & Kanwisher, 2014; Blank & Fedorenko, 2017; Paunov, Blank, & Fedorenko, 2019), the resulting fROIs showed small pairwise overlaps within individuals across networks, and overlapping voxels were excluded in fROI definition. In the current sample, the language-MD and ToM-MD overlaps were negligible, with a median overlap of 0 and average percentage overlap of less than 3% of voxels, on average across participants, relative to the total size of all fROIs in either network. Similarly, the language-ToM overlaps were also small relative to all fROIs in either network (6.3% of voxels, on average across participants, relative to the total number of voxels in language fROIs and 3.2% relative to all ToM fROIs). This overlap was localized entirely to one pair of fROIs: the LPostTemp language fROI and the LTPJ ToM fROI, and was more substantial relative to the total sizes of just these two fROIs: 38.6 voxels, on average across participants, i.e., 13.1% out of 295 total LPostTemp voxels, and 11.6% out of 332 total LTPJ voxels. We therefore repeated all key analyses without excluding these voxels in defining the fROIs. The results of these alternative analyses were qualitatively and statistically similar.

2.7. Reality check and replication analyses

Prior to performing our critical analyses, we conducted two reality-check analyses and—in line with increasing emphasis in the field on robust and replicable science (e.g., Poldrack et al., 2017)—an analysis aimed at replicating and extending a previous ISC-based finding from our lab (Blank & Fedorenko, 2017).

ISCs in perceptual cortices. Anatomical ROIs were additionally defined in early visual and auditory cortex in all participants. For visual cortex, regions included inferior, middle, and superior occipital cortex bilaterally (six ROIs in total; masks available from http://fmri.wfubmc.edu/software/PickAtlas). For auditory cortex, regions included posteromedial and anterolateral sections of Heschl's gyrus bilaterally (4 ROIs in total; Morosan et al., 2001; these regions are based on post-mortem histology, and have been used in a number of previous fMRI papers). Signal extraction, ISC estimation, and inferential statistics were performed identically to the critical analyses (see Section 2.8). ISCs from these regions were used in a reality check (see Section 3.1), to ensure a double-dissociation obtains between visually and auditorily presented conditions in these perceptual regions.

Resting state ISCs. A subset of ten participants (who completed 1-7 of the critical conditions) completed a resting state scan, which was included to ensure that data acquisition, preprocessing, and modelling procedures do not induce spurious ISCs. To this end, signal extraction, ISC estimation, and inferential statistics were performed identically to the critical analyses (see Section 2.8).

Replication analysis: Closer tracking of linguistic input by language regions than by domain-general Multiple Demand (MD) regions. Blank & Fedorenko (2017) reported stronger ISCs during the processing of naturalistic linguistic materials in the language regions, compared to domain-general Multiple Demand (MD) regions. The MD network has been implicated in executive processes and goal-directed behavior (e.g., Duncan, 2010, 2013), including in the domain of language (e.g., see Fedorenko, 2014, for a review; cf. Diachek, Blank, Siegelman et al., 2020; Fedorenko & Shain, under review). We sought to replicate Blank & Fedorenko's key result in a new set of participants and to extend it to different types of linguistic materials. Specifically, the original study used narratives, including the narrative used in the present study along with three others. We expected the results to generalize to non-narrative linguistic conditions. Ten participants in our dataset (n=6 in the narrative condition) who also participated in the original study were excluded from this analysis. Again, signal extraction, ISC estimation, and inferential statistics were identical to the critical analyses (see Section 2.8).

2.8. Critical analyses

Computing ISCs. For each participant and fROI, BOLD signal time courses recorded during each naturalistic condition were extracted from each voxel beginning 6 s following the onset of the stimulus (to exclude an initial rise in the hemodynamic response relative to fixation, which could increase ISCs) and averaged across voxels. For each fROI, participant, and condition we computed an ISC value, namely, Pearson's moment correlation coefficient between the z-scored time course and the corresponding z-scored and averaged time course across the remaining participants (Lerner et al., 2011). ISCs were Fisher-transformed before statistical testing to improve normality (Silver and Dunlap, 1987).

Statistical testing. In each fROI, ISCs were then tested for significance against an empirical null distribution based on 1,000 simulated signal time courses that were generated by phase-randomization of the original data (Theiler et al., 1992). Namely, we generated null distributions for individual participants, fit each distribution with a Gaussian, and analytically combined the resulting parameters across participants. The true ISCs, also averaged across participants, were then z-scored relative to these empirical parameters and converted to one-tailed *p*-values.

ISCs were compared across networks and condition types using linear, mixed-effects regressions, implemented in Matlab 2020a. ISCs were modeled with maximal random effects structure appropriate for each analysis (Barr et al., 2013; Baayen et al., 2008), including random intercepts for participants, with random slopes for the effects of interest, and crossed random intercepts for fROI and condition. Hypothesis testing was performed with two-tailed tests over the respective model coefficients, with Satterthwaite approximation for the degrees of freedom.

Further analyses performed within networks across condition types or against the theoretical null distribution (i.e., testing the intercept term), as well as those per fROI within a network or per condition across networks, also always included maximal random effects on the remaining grouping variables. P-values in these analyses are reported following false discovery rate (FDR) correction for multiple comparisons (Benjamini and Yekutieli, 2001).

Lastly, in comparisons against baseline, per-fROI analyses against empirical null distributions are also reported, which aim to ensure that, at the finest grain (each individual fROI and condition, across participants), differences from baseline are independent of assumptions regarding data normality. These tests were also FDR corrected for multiple comparisons for all fROIs within a network, and across all seven conditions of interest.

3. Results

3.1. Results of reality check and replication analyses

Reality check #1: ISCs in perceptual cortices. We examined ISCs for the conditions of interest in early auditory and visual cortex, grouping the conditions by presentation modality. As expected, we observed stronger ISCs for the auditory conditions in the auditory cortex, and stronger ISCs for the visual conditions in the visual cortex (**Figure 2**). The linear mixed-effects (LME) regression (see Methods) revealed a strong crossover interaction (beta = 0.648, SE = 0.046, $t(89.79) = 13.970$, $p = 10^{-25}$).

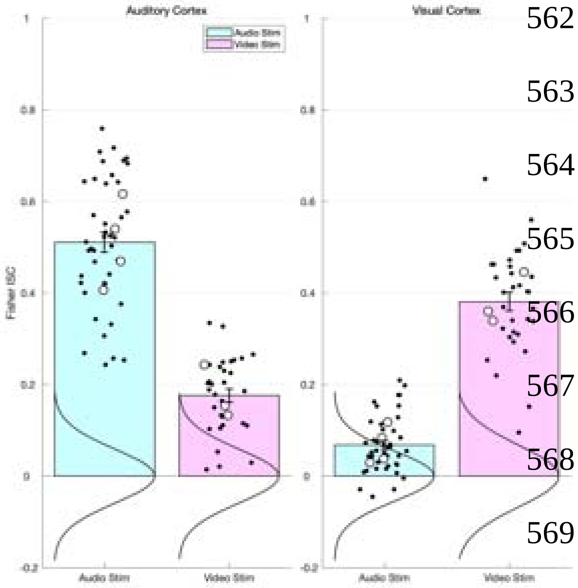


Figure 2. *A reality-check analysis showing the expected double dissociation in ISCs in perceptual (visual and auditory) cortices. Bars correspond to Fisher-transformed inter-subject correlation (ISC) coefficients (Pearson's r) in early visual and auditory cortex to the conditions of interest, grouped by modality of presentation (all +Language conditions: story, audio play, dialog, expository text were auditorily presented; the remaining conditions – animated short film, live action movie clip, and intentional shapes animation – were visually presented). Error bars are standard errors of the mean by participants. Black dots correspond to the individual participants' values. Large unfilled circles correspond to individual condition averages. Vertical curves are Gaussian fits to empirical null distributions.*

Notably, we also observed that the visual areas weakly but reliably tracked the auditory conditions (beta = 0.066, SE = 0.012, $t(38.10) = 5.398$, $p = 10^{-7}$), and the early auditory areas reliably tracked the visual conditions (beta = 0.175, SE = 0.020, $t(24.15) = 8.573$, $p = 10^{-10}$). We return to the interpretation of these effects in the Discussion. For the time being, we note that care must be taken in interpreting deviations of the ISCs during 'active' (cf. resting state) conditions from baseline.

Reality check #2: Resting state ISCs. To exclude the possibility that the ISCs in the critical analyses are driven by scanner noise or preprocessing/analysis procedures, we measured ISCs across a subset of ten participants who were scanned in a 5-minute resting state condition (Hasson et al., 2004). The ISCs during rest did not significantly differ from baseline in either the language or ToM networks, as assessed with an LME regression, or against the empirical null distribution. This analysis suggests that any above-baseline ISCs for our critical conditions are not an artifact of data acquisition, preprocessing, or analysis procedures.

Replication analysis: Closer tracking of linguistic input by language regions than by domain-general Multiple Demand (MD) regions. We successfully replicated the key finding for the narrative condition (beta = 0.181, SE = 0.039, $t(34.89) = 4.664$, $p = 10^{-5}$; p values are FDR-corrected for the four linguistic conditions), and extended it to the audio play (beta = 0.307, SE = 0.052, $t(34.23) = 5.944$, $p = 10^{-7}$), the dialogue (beta = 0.157, SE = 0.039, $t(33.05) = 4.014$, $p = 10^{-5}$), and the expository text (beta = 0.129, SE = 0.036, $t(36.75) = 3.543$, $p = 10^{-4}$) conditions (**Supplemental Figure A3**). These results suggest that across diverse kinds of linguistic stimuli, the language network's activity is more tightly coupled with the inputs, compared to the domain-general MD regions' activity.

3.2. Results of critical analyses

Evidence for dissociation between the language and ToM networks in direct network comparisons.

We tested three key predictions, which, if supported, provide evidence in favor of language-ToM dissociability in naturalistic settings. First, the ToM network should track conditions rich in ToM content irrespective of whether these conditions are linguistic or non-linguistic, whereas the language network should track linguistic conditions more strongly than non-linguistic ones. Indeed, we found a network (language, ToM) x condition type (*linguistic*: narrative, audio play, dialog, expository text; *non-linguistic*: animated film, live action film clip, Heider & Simmel-style animation) interaction (beta = 0.191, SE = 0.059, $t(84.06) = 3.270$, $p = 0.002$). We also found main effects of condition type and network: the linguistic conditions were—on average across networks—tracked more strongly than the non-linguistic conditions (beta = 0.124, SE = 0.0459, $t(96.47) = 2.700$, $p = 0.008$), and the language network tracked the conditions more strongly, on average, than the ToM network (beta = 0.096, SE = 0.039, $t(86.87) = 2.487$, $p = 0.015$).

Second, for non-linguistic conditions, the ToM network should exhibit stronger tracking of conditions with mental state content than the language network. Indeed, the ToM network showed higher ISCs than the language network (beta = 0.095, SE = 0.043, $t(35.59) = 2.197$, $p = 0.035$).

And third, for the linguistic condition without mental state content (the expository text), the language network should exhibit stronger tracking than the ToM network. Indeed, the language network showed higher ISCs than the ToM network (beta = 0.111, SE = 0.044, $t(19.10) = 2.507$, $p = 0.021$).

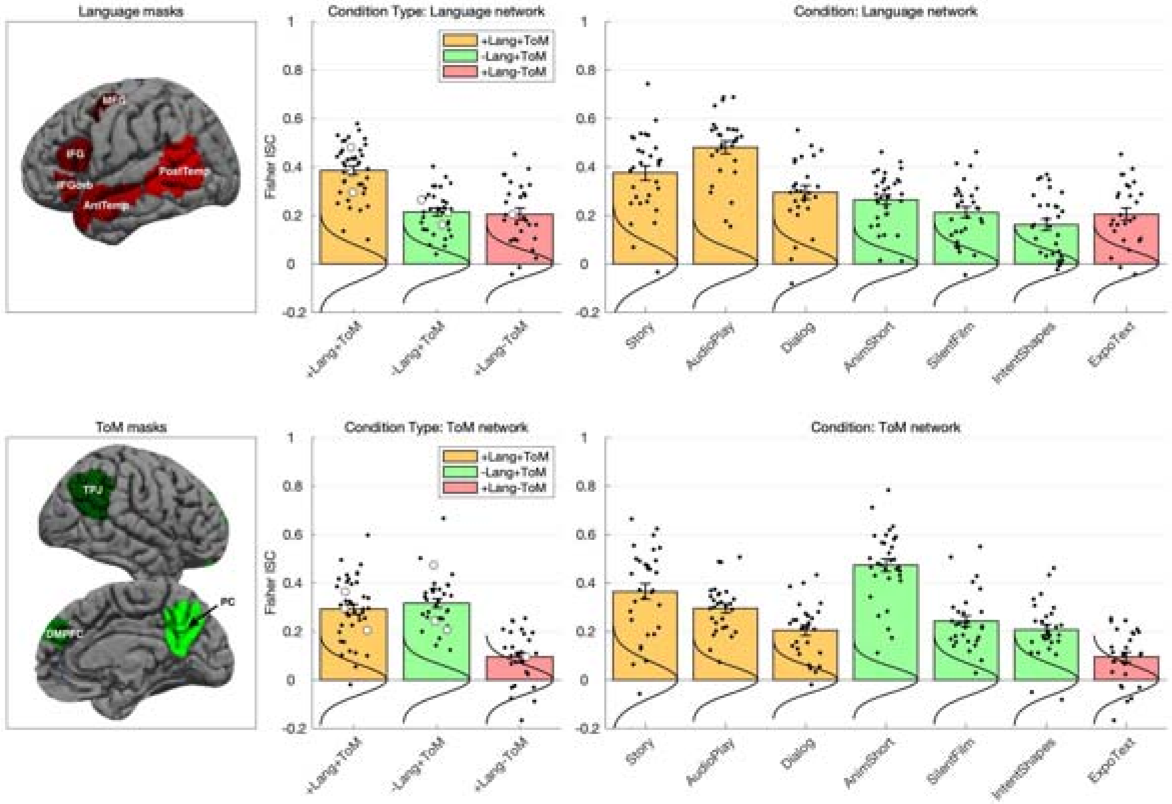


Figure 3. Left. *Masks within which individual functional regions of interest (fROIs) were defined for each network: Language (Top, red): IFGorb, inferior frontal gyrus, orbital portion; IFG, inferior frontal gyrus; MFG, middle frontal gyrus; AntTemp, anterior temporal cortex; PostTemp, posterior temporal cortex (only the classic, left-hemisphere language regions were included in all analyses). ToM (Bottom, green): TPJ, temporoparietal junction; DMPFC, dorsomedial prefrontal cortex; PC, posterior cingulate cortex and precuneus. Both the right-hemisphere (shown) and left-hemisphere ToM regions were included (six regions total).* ***Middle.***

Average inter-subject correlations (ISCs) per condition type in the language (top) and ToM (bottom) networks. Bars correspond to Fisher-transformed ISC coefficients (Pearson's r), averaged across regions of interest within each network, separately per condition. Colors represent condition types: +Lang+ToM, orange, -Lang+ToM, green, +Lang-ToM, red. Error bars are standard errors of the mean by participants. Black dots correspond to the individual participants' values. Large unfilled circles correspond to individual condition averages, shown individually in the right-most panels. Vertical curves are Gaussian fits to empirical null distributions. The key pattern is as follows. The ToM network tracks +ToM materials in both +Linguistic and -Linguistic conditions, but shows weak tracking of the -ToM stimulus. The language network preferentially tracks +Linguistic materials over -Linguistic ones, and it tracks +Linguistic materials in both +ToM and -ToM conditions. ***Right.*** *ISCs per individual naturalistic stimuli ('conditions'); conventions are as in middle panels.*

A more detailed characterization of the two networks' ISC profiles.

In this section, we examine more closely the detailed pattern of ISCs in the two networks of interest. The first aim of these analyses is to establish that the observed dissociation is not driven by particular conditions or regions within the networks, but rather, that different aspects of the data provide convergent support for the dissociation. The second aim is to highlight aspects of the ISC pattern that are not consistent with a complete language-ToM dissociation, and thus to evaluate the strength of counter-evidence in favor of the null hypothesis, that language and ToM are not dissociable in naturalistic cognition (see **Supplemental Figure B1** for ISCs per fROI for each network and condition).

ToM network. First, the ToM network reliably tracked each of the six conditions with mental state content: story (beta = 0.363, SE = 0.037, $t(26.55) = 9.693$, $p = 10^{-10}$); p values are FDR-corrected for seven conditions—we are including all conditions in the correction, not only the +ToM conditions), audio play (beta = 0.295, SE = 0.028, $t(10.54) = 10.716$, $p = 10^{-7}$), dialog (beta = 0.203, SE = 0.026, $t(16.40) = 7.797$, $p = 10^{-7}$), animated short (beta = 0.472, SE = 0.053, $t(9.35) = 8.830$, $p = 10^{-6}$), live action film (beta = 0.241, SE = 0.035, $t(11.18) = 6.869$, $p = 10^{-6}$), and Heider & Simmel (H&S) style animation (beta = 0.205, SE = 0.026, $t(15.72) = 7.838$, $p = 10^{-7}$). Moreover, in tests against the empirical null distributions these effects were significant in every ToM fROI with the exception of the Dialog condition in the RH Posterior Cignulate/Precuneus, (all other *ps* < 0.04, FDR-corrected for the six fROIs and seven conditions).

Second, the ToM network showed no preference for linguistic *vs.* non-linguistic conditions with mental state content (beta = 0.018, SE = 0.043, $t(49.74) = 0.675$, *n.s.*), consistent with these regions' role in representing mental states irrespective of how this information is conveyed (e.g., Jacoby et al., 2016).

And third, the ToM network tracked the linguistic conditions with mental state content (story, audio play, dialog) more strongly than the one without mental state content (expository text) (beta = 0.199, SE = 0.037, $t(30.69) = 5.344$, $p = 10^{-7}$), suggesting that the network represents mental state information in linguistic signals, rather than the linguistic signal itself. However, the ToM network did exhibit weaker but significantly above-baseline tracking of the expository text (beta = 0.093, *SE* = 0.022, *t*(22.22) = 4.165, *p* = 0.001). In per-fROI tests against the empirical null distributions, this effect was only reliable in the LTPJ (*p* = 0.015; all other *p*s > 0.05; FDR-corrected for the six fROIs). We consider possible explanations in the Discussion.

Language network. First, the language network reliably tracked each of the three linguistic conditions with mental state content: story (beta = 0.374, SE = 0.041, *t*(13.27) = 9.171, $p = 10^{-7}$; *p* values are FDR-corrected for seven conditions), audio play (beta = 0.479, *SE* = 0.046, *t*(8.75) = 10.370, $p = 10^{-6}$), and dialog (*r* = 0.294, *SE* = 0.045, *t*(9.72) = 6.491, $p = 10^{-4}$). Moreover, these effects were significant in every language fROI, in tests against the empirical null distributions (*p*s < 0.01, FDR-corrected for the five fROIs and seven conditions).

Second, importantly, the language network also reliably tracked the linguistic condition with no mental state content (beta = 0.204, *SE* = 0.044, *t*(8.72) = 4.668, $p = 10^{-4}$), and this effect, too, was significant in every language fROI (*p*s < 0.03, FDR-corrected for the five fROIs). This result suggests that mental state content is not necessary to elicit reliable ISCs in the language network.

And third, the language network showed stronger tracking of linguistic relative to non-linguistic conditions with mental state content, (beta = 0.177, SE = 0.043, *t*(43.54) = 4.155, $p = 10^{-5}$). This result suggests a special role for linguistic input in driving the network's responses.

However, the language network exhibited some patterns that might be taken to suggest that mental state content—or social information more generally—is, to some extent, important for linguistic processing. First, the language network tracked the linguistic conditions with mental state content more strongly than the linguistic condition with no mental state content, i.e., the expository text (beta = 0.188, SE = 0.061, $t(25.67) = 3.050$, $p = 0.005$). This result may be taken to suggest that mental state content contributes to the language network's input tracking over and above the linguistic content alone. This interpretation warrants caution, however. In particular, reflecting the general challenges of naturalistic stimuli (see Discussion), the linguistic condition with no mental state content is not matched to the linguistic conditions with mental state content on various potentially relevant features, from how engaging they are, which could influence the depth of linguistic encoding, to specifically linguistic properties (e.g., lexical and syntactic complexity), which could also affect the strength of ISCs (e.g., Shain, Blank et al., 2020; Wehbe et al., 2021). Furthermore, only a single linguistic condition with no mental state content was included in the current study, making it difficult to rule out idiosyncratic features driving the difference.

And second, the above-baseline ISCs in the language network for the non-linguistic conditions—although weaker than those for the linguistic conditions—are also notable, suggesting some degree of reliable tracking in the language network for non-linguistic meaningful information (see also Ivanova et al., 2020 for evidence of reliable responses in the language network to visual events).

4. Discussion

Much prior work in cognitive neuroscience has suggested—based on traditional controlled experimental paradigms—that the network of brain regions that support linguistic interpretation and the brain regions that support mental state reasoning are distinct (e.g., Saxe & Kanwisher, 2003; Mason & Just, 2009; Fedorenko et al., 2011; Mar, 2011; Deen et al., 2015; Paunov, 2019). However, such paradigms differ drastically from real-world cognition, where we process rich and complex information. And linguistic and social cognition seem to be strongly intertwined in everyday life. Here, we tested whether the language and Theory of Mind networks are dissociated in their functional profiles as assessed using the inter-subject correlation (ISC) approach, where neural activity patterns are correlated across individuals during the processing of naturalistic materials (e.g., Hasson et al., 2004, 2008). Following Blank & Fedorenko (2017), we combined the ISC approach with the power of individual-participant functional localization (e.g., Brett et al., 2002; Saxe et al., 2006; Fedorenko et al., 2010; Nieto-Castañón & Fedorenko, 2012). This synergistic combination has two key advantages over the whole-brain voxel-wise ISC approach, where individual brains are first anatomically aligned and, then, each stereotaxic location serves as a basis for comparing signal time courses across participants. First, relating the resulting cortical topography of ISCs to the topography of known functional brain networks can only proceed only through "reverse inference" based on anatomy (Poldrack, 2006; Fedorenko, 2021). Instead, evaluating signal time courses from functionally defined regions ensures interpretability, and allows us to straightforwardly link our findings to the wealth of prior studies characterizing the response profiles of our two networks of interest. And second, this approach allows us to directly test the correlations in the language network against those in the ToM network. Such an explicit comparison between networks allows for stronger inferences compared with those licensed when each network is separately tested against a null baseline and differences across networks are indirectly inferred (e.g., see Nieuwenhuis et al., 2011, for discussion).

We examined the ISCs in the language and ToM networks during the processing of seven naturalistic conditions: three linguistic conditions with mental state content (+linguistic, +ToM), three non-linguistic conditions (silent animations and live action films) with social content but no language (-linguistic, +ToM), and a linguistic condition with no social content (+linguistic, -ToM). We found reliable differences in the ISC patterns between the language and ToM networks, in support of the hypothesis that language and Theory of Mind are dissociable even during the processing of rich and complex naturalistic materials. In particular, the ToM network tracked materials rich in mental state content irrespective of whether this content was presented linguistically or non-linguistically (see also Jacoby et al., 2016), but it showed only weak tracking of the stimulus with no mental state content. In contrast, the language network preferentially tracked linguistic materials over non-linguistic ones, and it did so regardless of whether these materials contained information about mental states.

These results expand on the existing body of knowledge about language and social cognition, with both theoretical and methodological implications. Critically, the observed dissociation extends prior findings of dissociable functional profiles between the language and the ToM networks during task-based paradigms to rich naturalistic conditions. This result suggests that the two networks represent *different kinds of information*. (They may also perform *distinct computations* on the perceptual inputs, though the idea of a canonical computation carried out across the cortex is gaining ground (e.g., Keller & Mrsic-Flogel, 2018), and predictive processing seems like one likely candidate (e.g., Koster-Hale & Saxe, 2013; Shain, Blank et al., 2020). In particular, the language regions appear to track linguistic features of the input (see also Shain, Blank et al., 2020; Wehbe et al., 2021). Our results extend prior findings from ISC paradigms (Wilson et al., 2008; Lerner et al., 2011; Honey et al., 2012; Regev et al., 2013; Silbert et al., 2014; Schmälzle et al., 2015; Blank & Fedorenko, 2017), which all used materials rich in mental state content, as is typical of linguistic information, to a stimulus that is largely devoid of information about mental states—an expository text. Strong tracking of the latter stimulus aligns with prior findings from task-based paradigms of robust responses to linguistic materials with little or no mental state content (e.g., Deen et al., 2015; Jacoby & Fedorenko, 2020). The ToM regions, in contrast, appear to track some features related to representing mental states across diverse kinds of representations (linguistic materials, animations, including highly abstract and minimalistic ones, and live action movies), again aligning with prior findings from task-based paradigms (e.g., Fletcher et al., 1995; Gallagher et al., 2000; Castelli et al., 2000; Vogeley et al., 2001; Ruby & Decety, 2003; Saxe & Kanwisher, 2003; Saxe, Schulz, & Jiang, 2006; Jacoby et al., 2016). It is important to keep in mind that the fact that the two networks are dissociable does not imply that they do not interact. Indeed, Paunov et al. (2019) reported reliably above chance correlations in the patterns of inter-regional synchronization between the language and ToM networks, suggesting some degree of functional integration.

On the methodological level, these results vindicate the divide-and-conquer strategy in general, and the functional localization approach (e.g., Brett et al., 2002; Saxe et al., 2006; Fedorenko et al., 2010) in particular. Language and Theory of Mind appear to be natural kinds, and the networks supporting the processing of linguistic vs. mental state information appear to be distinct, at least in adulthood (see also Braga et al., 2020). It is therefore justifiable to study each cognitive faculty and each network separately, although further probing the mechanisms of their potential interactions is equally important.

Although the overall pattern clearly supports a language-ToM dissociation between the two networks, some aspects of the results are not in line with a complete dissociation. In particular, i) the language regions show reliable tracking of non-linguistic conditions with mental state content; ii) the language regions show stronger tracking of linguistic conditions with than without mental state content; and iii) the ToM regions show weak but reliable tracking of the linguistic condition with no mental state content. These findings may be due to methodological limitations: the above-baseline ISCs (especially the relatively weak ones) may not reflect stimulus tracking. Although we have ruled out the possibility that the above-baseline ISCs are driven by acquisition, preprocessing, or analysis artifacts in our reality-check analysis of resting state data, they could be driven by other factors. For example, inter-network interactions (see Paunov et al., 2019) could induce ISCs, or the stimuli themselves may be too confounded to dissociate the respective contributions of language- and ToM-related components (for example, in linguistic stimuli, mental state attribution often requires particular syntactic structures—sentential complements).

More generally, the use of naturalistic materials, despite its advantages (e.g., Hasson et al., 2018; Sonsukare et al., 2019; Nastase et al., 2020), is associated with a host of challenges. The key one is that certain features are necessarily confounded in naturalistic settings, and can only be dissociated through careful experimentation and altering the natural statistics of the input. Relying on naturalistic materials alone can lead to wrong conclusions about the cognitive and neural architecture. This problem is especially pronounced in studying the relationship between language and social cognition given that language is primarily used in social settings and to share socially relevant information. The use of linguistic materials with no social information, and of non-linguistic mental-state-rich materials has been critical, here and in earlier studies, to uncover the dissociation that holds between the language and ToM systems. Another challenge associated with naturalistic materials is that they are difficult or altogether impossible to match for diverse properties bound to affect neural responses. Again, this problem presents a particular challenge in comparing responses to materials rich in social information vs. devoid of such information given that the former are, almost by definition, going to be more engaging and exciting given the social nature of primates, including humans (e.g., Aronson, 1980; Cheney & Seyfarth, 1990; Tomasello, 2014). Possible ways to address some of these concerns could involve a) characterizing the natural statistics of co-occurrences between linguistic and social processing in order to better understand how well the naturalistic stimuli reflect those statistics and to perhaps altering naturalistic conditions to allow dissociating features that commonly co-occur in life; b) carefully annotating naturalistic materials and performing reverse correlation analyses (e.g., Hasson et al., 2004; Jacoby et al., 2016) in an effort to understand the precise features that elicit increases in neural responses in different brain regions; and c) developing novel neural analysis methods to isolate the components of neural signals attributable to a particular cognitive process / brain network (e.g., using analytic methods well-suited to high-dimensional data such as independent components analysis across both cortical space and large feature spaces representative of naturalistic environments (e.g., Norman-Haignere et al., 2015), or across both cortical space and time (e.g., probabilistic ICA, PICA; see Beckmann et al., 2005 for overview).

Finally, this work leaves open a number of exciting future directions, some of which may build directly on the approaches introduced and the findings reported in the current study. First, the language and ToM networks appear to be dissociable in the adult mind and brain. However, it is possible—perhaps even plausible—that this dissociation emerges over the course of development. Prior neuroimaging work has shown that the ToM network becomes gradually more specialized for mental state attribution (e.g., Saxe, 2009; Gweon et al., 2012; Richardson et al., 2018), and this specialization appears to be delayed with delayed language acquisition (Richardson et al., 2020). And very little is known about how specialization for linguistic processing (e.g., Fedorenko et al., 2011; Monti et al., 2012) emerges. Perhaps early on in development, a set of lateral frontal, lateral temporal, and midline cortical areas are tuned to *any* socially relevant information, and these areas later fractionate into those specialized for processing linguistic signals vs. those for mental state attribution vs. those that support many other kinds of social signals, from eye gaze, to facial expressions, to body postures, to prosody, to gestures (e.g., Downing et al., 2006; Deen et al., 2015; Isik et al., 2017; Jouravlev et al., 2019). This fractionation is likely driven by computational and metabolic advantages of localized processing (e.g., Barlow, 1995; Foldiak & Young, 1995; Chklovskii & Koulakov, 2004; Olshausen & Field, 2004; see Kanwisher, 2010, for discussion). Probing linguistic and social cognition across the lifespan will be critical to understand how the two networks form and develop, leading to the segregation we observe in the adult brain.

Second, as noted above, given the likely frequent interactions between the language and ToM networks (including their most strongly dissociated components), searching for possible mechanisms of those interactions (e.g., Paunov et al., 2019) seems critical. This would require a combination of studies characterizing the patterns of anatomical connections for the language and ToM regions (e.g., Saur et al., 2010; Wiesmann et al., 2017) and studies probing online interactions using methods with high temporal resolution, like MEG or intracranial recordings.

And third, we are still a long way away from a mechanistic-level understanding of what the language or the ToM regions do. The use of naturalistic stimuli, including in the context of the ISC approach, is promising. In particular, by examining the points in the stimulus where most participants show increases in neural activity can help generate (and subsequently test) specific hypotheses about the necessary and sufficient features of the input required to elicit neural responses in the relevant brain regions.

To conclude, we have demonstrated that the dissociation between the language and ToM networks that has been previously reported based on traditional task paradigms, robustly generalizes to rich naturalistic conditions. However, the precise nature of each network’s representations and computations, the emergence of these networks from birth to adulthood, and the mechanisms for information sharing between them remain to be discovered.

References

Amalric, M., & Dehaene, S. (2018). Cortical circuits for mathematical knowledge: evidence for a major subdivision within the brain's semantic networks. *Philosophical Transactions of the Royal Society B: Biological Sciences, 373*(1740), 20160515.

Anderson, A. J., Lalor, E. C., Lin, F., Binder, J. R., Fernandino, L., Humphries, C. J., ... & Wang, X. (2019). Multiple regions of a cortical network commonly encode the meaning of words in multiple grammatical positions of read sentences. *Cerebral cortex, 29*(6), 2396-2411.

Apperly, I. A., Samson, D., Carroll, N., Hussain, S., & Humphreys, G. (2006). Intact first-and second-order false belief reasoning in a patient with severely impaired grammar. *Social neuroscience, 1*(3-4), 334-348.

Aronson E. The social animal. New York: Palgrave Macmillan; 1980.

Ayyash, D., Malik-Moraleda, S., Gallée, J., Affourtit, J., Mineroff, Z., Jouravlev, O., & Fedorenko, E. (in prep). The universal language network: A cross-linguistic investigation spanning 45 languages and 11 language families.

Baayen, R. H., Davidson, D. J., & Bates, D. M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. *Journal of memory and language, 59*(4), 390-412.

Barlow, H. (1995). The neuron doctrine in perception.

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. Journal of memory and language, 68(3), 255-278.

Bautista, A., & Wilson, S. M. (2016). Neural responses to grammatically and lexically degraded speech. *Language, cognition and neuroscience, 31*(4), 567-574.

Beckmann, C. F., DeLuca, M., Devlin, J. T., & Smith, S. M. (2005). Investigations into resting-state connectivity using independent component analysis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *360*(1457), 1001-1013.

Bedny, M., Pascual-Leone, A., Dodell-Feder, D., Fedorenko, E., & Saxe, R. (2011). Language processing in the occipital cortex of congenitally blind adults. *Proceedings of the National Academy of Sciences*, *108*(11), 4429-4434.

Benjamini, Y., & Yekutieli, D. (2001). The control of the false discovery rate in multiple testing under dependency. *The annals of statistics*, *29*(4), 1165-1188.

Blank, I. A., & Fedorenko, E. (2017). Domain-general brain regions do not track linguistic input as closely as language-selective regions. *Journal of Neuroscience*, *37*(41), 9999-10011.

Blank, I., Balewski, Z., Mahowald, K., & Fedorenko, E. (2016). Syntactic processing is distributed across the language system. *Neuroimage*, *127*, 307-323.

Blank, I., Kanwisher, N., & Fedorenko, E. (2014). A functional dissociation between language and multiple-demand systems revealed in patterns of BOLD signal fluctuations. *Journal of neurophysiology*, *112*(5), 1105-1118.

Bower, G. H., & Morrow, D. G. (1990). Mental models in narrative comprehension. *Science*, *247*(4938), 44-48.

Braga, R. M., DiNicola, L. M., Becker, H. C., & Buckner, R. L. (2020). Situating the left-lateralized language network in the broader organization of multiple specialized large-scale distributed networks. *Journal of neurophysiology*, *124*(5), 1415-1448.

Brett, M., Johnsrude, I. S., & Owen, A. M. (2002). The problem of functional localization in the human brain. *Nature reviews neuroscience*, *3*(3), 243.

Bruneau, E. G., Pluta, A., & Saxe, R. (2012). Distinct roles of the ‘shared pain’ and ‘theory of mind’networks in processing others’ emotional suffering. *Neuropsychologia*, *50*(2), 219-231.

Callaghan, T., Rochat, P., Lillard, A., Claux, M. L., Odden, H., Itakura, S., ... & Singh, S. (2005). Synchrony in the onset of mental-state reasoning: Evidence from five cultures. *Psychological Science*, *16*(5), 378-384.

Castelli, F., Happé, F., Frith, U., & Frith, C. (2000). Movement and mind: a functional imaging study of perception and interpretation of complex intentional movement patterns. *Neuroimage*, *12*(3), 314-325.

Chen, G., Taylor, P. A., & Cox, R. W. (2017). Is the statistic value all we should care about in neuroimaging?. *Neuroimage*, *147*, 952-959.

Cheney, D., & Seyfarth, R. (1990). Attending to behaviour versus attending to knowledge: Examining monkeys' attribution of mental states. *Animal Behaviour*, *40*(4), 742-753.

Chklovskii, D. B., & Koulakov, A. A. (2004). Maps in the brain: what can we learn from them?. *Annu. Rev. Neurosci.*, *27*, 369-392.

Cordes, D., Haughton, V. M., Arfanakis, K., Carew, J. D., Turski, P. A., Moritz, C. H., ... & Meyerand, M. E. (2001). Frequencies contributing to functional connectivity in the cerebral cortex in “resting-state” data. *American Journal of Neuroradiology*, *22*(7), 1326-1333.

Cuevas, P., Steines, M., He, Y., Nagels, A., Culham, J., & Straube, B. (2019). The facilitative effect of gestures on the neural processing of semantic complexity in a continuous narrative. *NeuroImage*, *195*, 38-47.

Deen, B., Koldewyn, K., Kanwisher, N., & Saxe, R. (2015). Functional organization of social perception and cognition in the superior temporal sulcus. *Cerebral Cortex*, bhv111.

Diachek, E., Blank, I., Siegelman, M., Affourtit, J., & Fedorenko, E. (2020). The domain-general multiple demand (MD) network does not support core aspects of language comprehension: a large-scale fMRI investigation. *Journal of Neuroscience, 40*(23), 4536-4550.

Downing, P. E., Peelen, M. V., Wiggett, A. J., & Tew, B. D. (2006). The role of the extrastriate body area in action perception. Social Neuroscience, 1(1), 52-62.

Dufour, N., Redcay, E., Young, L., Mavros, P. L., Moran, J. M., Triantafyllou, C., ... & Saxe, R. (2013). Similar brain activation during false belief tasks in a large sample of adults with and without autism. *PloS one*, *8*(9), e75468.

Dunbar, R. I. (2004). Gossip in evolutionary perspective. *Review of general psychology*, *8*(2), 100-110.

Dunbar, R. I., Marriott, A., & Duncan, N. D. (1997). Human conversational behavior. *Human nature*, *8*(3), 231-246.

Duncan, J. (2010). The multiple-demand (MD) system of the primate brain: mental programs for intelligent behaviour. *Trends in cognitive sciences*, *14*(4), 172-179.

Duncan, J. (2013). The structure of cognition: attentional episodes in mind and brain. *Neuron*, *80*(1), 35-50.

Fedorenko, E. (2021). The early origins and the growing popularity of the individual-subject analytic approach in human neuroscience. *Current Opinion in Behavioral Sciences*, *40*, 105-112.

Fedorenko, E. (2014). The role of domain-general cognitive control in language comprehension. *Frontiers in psychology*, *5*, 335.

Fedorenko, E., Behr, M. K., & Kanwisher, N. (2011). Functional specificity for high-level linguistic processing in the human brain. *Proceedings of the National Academy of Sciences*, *108*(39), 16428-16433.

Fedorenko, E., Blank, I. A., Siegelman, M., & Mineroff, Z. (2020). Lack of selectivity for syntax relative to word meanings throughout the language network. *Cognition*, *203*, 104348.

Fedorenko, E., Duncan, J., & Kanwisher, N. (2013). Broad domain generality in focal regions of frontal and parietal cortex. *Proceedings of the National Academy of Sciences*, *110*(41), 16616-16621.

Fedorenko, E., Hsieh, P. J., Nieto-Castañón, A., Whitfield-Gabrieli, S., & Kanwisher, N. (2010). New method for fMRI investigations of language: defining ROIs functionally in individual subjects. *Journal of neurophysiology*, *104*(2), 1177-1194.

Fedorenko, E., & Kanwisher, N. (2009). Neuroimaging of language: why hasn't a clearer picture emerged?. *Language and Linguistics Compass*, *3*(4), 839-865.

Fedorenko, E., Mineroff, Z., Siegelman, M., & Blank, I. (2017). The distinction between lexico-semantic and syntactic processing is not an organizing dimension of the human language system. In *30th CUNY Conference on Human Sentence Processing, Cambridge, MA*.

Fedorenko, E., Nieto-Castanon, A., & Kanwisher, N. (2012b). Lexical and syntactic representations in the brain: an fMRI investigation with multi-voxel pattern analyses. *Neuropsychologia*, *50*(4), 499-513.

Fedorenko, E., Scott, T. L., Brunner, P., Coon, W. G., Pritchett, B., Schalk, G., & Kanwisher, N. (2016). Neural correlate of the construction of sentence meaning. *Proceedings of the National Academy of Sciences*, *113*(41), E6256-E6262.

Fedorenko & Shain (under review). Local implementation of general computations: The case of human language comprehension.

Fedorenko, E., & Thompson-Schill, S. L. (2014). Reworking the language network. *Trends in cognitive sciences*, *18*(3), 120-126.

Fedorenko, E., & Varley, R. (2016). Language and thought are not the same thing: evidence from neuroimaging and neurological patients. *Annals of the New York Academy of Sciences*, *1369*(1), 132.

Finlayson, M. A., & Winston, P. H. (2011). Narrative is a Key Cognitive Competency. In *BICA* (p. 110).

Fischl, B., Rajendran, N., Busa, E., Augustinack, J., Hinds, O., Yeo, B. T., ... & Zilles, K. (2007). Cortical folding patterns and predicting cytoarchitecture. *Cerebral cortex*, *18*(8), 1973-1980.

Fletcher, P. C., Happe, F., Frith, U., Baker, S. C., Dolan, R. J., Frackowiak, R. S., & Frith, C. D. (1995). Other minds in the brain: a functional imaging study of “theory of mind” in story comprehension. *Cognition*, *57*(2), 109-128.

Fodor, J. A. (1983). *The modularity of mind*. MIT press.

Foldiak, P., & Young, M. (1995). Sparse coding in the primate cortex. The Handbook of Brain Theory and Neural Networks, 895-898.

Frith, U., & Happé, F. (1994). Autism: beyond “theory of mind”. *Cognition*, *50*(1), 115-132.

from neuroimaging and neurological patients. *Annals of the New York Academy of Sciences*, *1369(1)*, 132-153.

Frost, M. A., & Goebel, R. (2012). Measuring structural–functional correspondence: spatial variability of specialised brain regions after macro-anatomical alignment. *Neuroimage*, *59*(2), 1369-1381.

Frost, M. A., & Goebel, R. (2012). Measuring structural–functional correspondence: spatial variability of specialised brain regions after macro-anatomical alignment. *Neuroimage*, *59*(2), 1369-1381.

Futrell, R., Gibson, E., Tily, H., Blank, I., Vishnevetsky, A., Piantadosi, S. T., & Fedorenko, E. (2017). The natural stories corpus. *arXiv preprint arXiv:1708.05763*.

Gallagher, H. L., Happé, F., Brunswick, N., Fletcher, P. C., Frith, U., & Frith, C. D. (2000). Reading the mind in cartoons and stories: an fMRI study of 'theory of mind'in verbal and nonverbal tasks. *Neuropsychologia*, *38*(1), 11-21.

Gallivan, J. P., Cavina-Pratesi, C., & Culham, J. C. (2009). Is that within reach? fMRI reveals that the human superior parieto-occipital cortex encodes objects reachable by the hand. *Journal of Neuroscience*, *29*(14), 4381-4391.

Grice, H. P. (1968). Utterer's meaning, sentence-meaning, and word-meaning. In *Philosophy, Language, and Artificial Intelligence* (pp. 49-66). Springer, Dordrecht.

Grice, H. P., Cole, P., & Morgan, J. (1975). Logic and conversation. *1975*, 41-58.

Gweon, H., Dodell□Feder, D., Bedny, M., & Saxe, R. (2012). Theory of mind performance in children correlates with functional specialization of a brain region for thinking about thoughts. *Child development*, *83*(6), 1853-1868.

Hasson, U., Egidi, G., Marelli, M., & Willems, R. M. (2018). Grounding the neurobiology of language in first principles: The necessity of non-language-centric explanations for language comprehension. *Cognition*, *180*, 135-157.

Hasson, U., Furman, O., Clark, D., Dudai, Y., & Davachi, L. (2008). Enhanced intersubject correlations during movie viewing correlate with successful episodic encoding. *Neuron*, *57*(3), 452-462.

Hasson, U., Malach, R., & Heeger, D. J. (2010). Reliability of cortical activity during natural stimulation. *Trends in cognitive sciences*, *14*(1), 40-48.

Hasson, U., Nir, Y., Levy, I., Fuhrmann, G., & Malach, R. (2004). Intersubject synchronization of cortical activity during natural vision. *science*, *303*(5664), 1634-1640.

HBO (Producer). (2003, December 7). Chapter 1: Bad News [Audio only]. *Angels in America*. Retrieved from https://www.imdb.com/title/tt0318997/

Heider, F., & Simmel, M. (1944). An experimental study of apparent behavior. *The American journal of psychology*, *57*(2), 243-259.

Honey, C. J., Thompson, C. R., Lerner, Y., & Hasson, U. (2012). Not lost in translation: neural responses shared across languages. *Journal of Neuroscience*, *32*(44), 15277-15283.

Isik, L., Koldewyn, K., Beeler, D., & Kanwisher, N. (2017). Perceiving social interactions in the posterior superior temporal sulcus. *Proceedings of the National Academy of Sciences*, *114*(43), E9145-E9152.

Ivanova, A. A., Mineroff, Z., Zimmerer, V., Kanwisher, N., Varley, R., & Fedorenko, E. (2021). The language network is recruited but not required for nonverbal event semantics. *Neurobiology of Language*, *2*(2), 176-201.

Ivanova, A. A., Siegelman, M., Cheung, C., Pongos, A. L. A., Kean, H. H., & Fedorenko, E. (in prep). The effect of task on sentence processing in the brain.

Ivanova, A. A., Srikant, S., Sueoka, Y., Kean, H. H., Dhamala, R., O'reilly, U. M., ... & Fedorenko, E. (2020). Comprehension of computer code relies primarily on domain-general executive brain regions. *Elife*, *9*, e58906.

Jacoby, N., & Fedorenko, E. (2020). Discourse-level comprehension engages medial frontal Theory of Mind brain regions even for expository texts. *Language, Cognition and Neuroscience*, *35*(6), 780-796.

Jacoby, N., Bruneau, E., Koster-Hale, J., & Saxe, R. (2016). Localizing Pain Matrix and Theory of Mind networks with both verbal and non-verbal stimuli. *Neuroimage*, *126*, 39-48.

Jouravlev, O., Zheng, D., Balewski, Z., Pongos, A. L. A., Levan, Z., Goldin-Meadow, S., & Fedorenko, E. (2019). Speech-accompanying gestures are not processed by the language-processing mechanisms. *Neuropsychologia*, 107132.

Julian, J. B., Fedorenko, E., Webster, J., & Kanwisher, N. (2012). An algorithmic method for functionally defining regions of interest in the ventral visual pathway. *Neuroimage, 60*(4), 2357-2364.

Kanwisher, N. (2010). Functional specificity in the human brain: a window into the functional architecture of the mind. *Proceedings of the National Academy of Sciences*, *107*(25), 11163-11170.

Keller, G. B., & Mrsic-Flogel, T. D. (2018). Predictive processing: a canonical cortical computation. *Neuron*, *100*(2), 424-435.

Koster-Hale, J., & Saxe, R. (2013). Functional neuroimaging of theory of mind. *Understanding other minds: Perspectives from developmental social neuroscience*, 132-163.

Koster-Hale, J., Bedny, M., & Saxe, R. (2014). Thinking about seeing: Perceptual sources of knowledge are encoded in the theory of mind brain regions of sighted and blind adults. *Cognition*, *133*(1), 65-78.

Lerner, Y., Epshtein, B., Ullman, S., & Malach, R. (2008). Class information predicts activation by object fragments in human object areas. *Journal of Cognitive Neuroscience*, *20*(7), 1189-1206.

Lerner, Y., Honey, C. J., Silbert, L. J., & Hasson, U. (2011). Topographic mapping of a hierarchy of temporal receptive windows using a narrated story. *Journal of Neuroscience*, *31*(8), 2906-2915.

Mar, R. A. (2011). The neural bases of social cognition and story comprehension. *Annual review of psychology*, *62*, 103-134.

Mason, R. A., & Just, M. A. (2009). The role of the theory□of□mind cortical network in the comprehension of narratives. *Language and Linguistics Compass*, *3*(1), 157-174.

Mellem, M. S., Jasmin, K. M., Peng, C., & Martin, A. (2016). Sentence processing in anterior superior temporal cortex shows a social-emotional bias. *Neuropsychologia*, *89*, 217-224.

Monti, M. M., Parsons, L. M., & Osherson, D. N. (2012). Thought beyond language neural dissociation of algebra and natural language. *Psychological Science*, 0956797612437427.

Morosan, P., Rademacher, J., Schleicher, A., Amunts, K., Schormann, T., & Zilles, K. (2001). Human primary auditory cortex: cytoarchitectonic subdivisions and mapping into a spatial reference system. *Neuroimage*, *13*(4), 684-701.

Mr Bean. (2009, Aug 25). *Falling Asleep in Church | Funny Clip | Mr Bean Official* [Video file]. Retrieved from https://www.youtube.com/watch?v=bh__g-ZZ6WA

Nastase, S. A., Goldstein, A., & Hasson, U. (2020). Keep it real: rethinking the primacy of experimental control in cognitive neuroscience. *NeuroImage, 222*, 117254.

Nieto-Castañón, A., & Fedorenko, E. (2012). Subject-specific functional localizers increase sensitivity and functional resolution of multi-subject analyses. *Neuroimage*, *63*(3), 1646-1669.

Nieuwenhuis, S., Forstmann, B. U., & Wagenmakers, E. J. (2011). Erroneous analyses of interactions in neuroscience: a problem of significance. *Nature neuroscience*, *14*(9), 1105.

Norman-Haignere, S., Kanwisher, N. G., & McDermott, J. H. (2015). Distinct cortical pathways for music and speech revealed by hypothesis-free voxel decomposition. *Neuron*, *88*(6), 1281-1296.

Nowak, M. A., & Sigmund, K. (2005). Evolution of indirect reciprocity. *Nature*, *437*(7063), 1291.

Nowak, M., & Highfield, R. (2011). *Supercooperators: Altruism, evolution, and why we need each other to succeed*. Simon and Schuster.

Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, *9*(1), 97-113.

Olshausen, B. A., & Field, D. J. (2004). Sparse coding of sensory inputs. *Current opinion in neurobiology*, *14*(4), 481-487.

Paunov A.M., Shain, C., Chen, J., Affourtit, J. & Fedorenko, E. (in prep). Spatial overlap between language and Theory of Mind networks with verbal but not with non-verbal tasks: fMRI evidence for dissociability.

Paunov, A. M., Blank, I. A., & Fedorenko, E. (2019). Functionally distinct language and Theory of Mind networks are synchronized at rest and during language comprehension. *Journal of neurophysiology*, *121*(4), 1244-1265.

Paunov, A.M. (2019). fMRI studies of the relationship between language and theory of mind in adult cognition. PhD Dissertation. Massachusetts Institute of Technology. Cambridge, MA, USA.

Piantadosi, S. T., Tily, H., & Gibson, E. (2011). Word lengths are optimized for efficient communication. *Proceedings of the National Academy of Sciences*, *108*(9), 3526-3529.

Poldrack, R. A. (2006). Can cognitive processes be inferred from neuroimaging data?. *Trends in cognitive sciences*, *10*(2), 59-63.

Poldrack, R. A., Baker, C. I., Durnez, J., Gorgolewski, K. J., Matthews, P. M., Munafò, M. R., ... & Yarkoni, T. (2017). Scanning the horizon: towards transparent and reproducible neuroimaging research. *Nature Reviews Neuroscience*, *18*(2), 115.

Pritchett, B. L., Hoeflin, C., Koldewyn, K., Dechter, E., & Fedorenko, E. (2018). High-level language processing regions are not engaged in action observation or imitation. *Journal of neurophysiology*, *120*(5), 2555-2570.

Redcay, E., Velnoskey, K. R., & Rowe, M. L. (2016). Perceived communicative intent in gesture and language modulates the superior temporal sulcus. *Human brain mapping*, *37*(10), 3444-3461.

Reddy, A. J., & Wehbe, L. (2020). Syntactic representations in the human brain: beyond effort-based metrics. *bioRxiv*.

Regev, M., Honey, C. J., Simony, E., & Hasson, U. (2013). Selective and invariant neural responses to spoken and written narratives. *Journal of Neuroscience*, *33*(40), 15978-15988.

Richardson, H., Koster-Hale, J., Caselli, N., Magid, R., Benedict, R., Olson, H., ... & Saxe, R. (2020). Reduced neural selectivity for mental states in deaf children with delayed exposure to sign language. *Nature communications*, *11*(1), 1-13.

Richardson, H., Lisandrelli, G., Riobueno-Naylor, A., & Saxe, R. (2018). Development of the social brain from age three to twelve years. *Nature communications*, *9*(1), 1-12.

Sabbagh, M. A., Xu, F., Carlson, S. M., Moses, L. J., & Lee, K. (2006). The development of executive functioning and theory of mind: A comparison of Chinese and US preschoolers. *Psychological science*, *17*(1), 74-81.

Saur, D., Schelter, B., Schnell, S., Kratochvil, D., Küpper, H., Kellmeyer, P., ... & Mader, W. (2010). Combining functional and anatomical connectivity reveals brain networks for auditory language comprehension. *Neuroimage*, *49*(4), 3187-3197.??

Saxe, R. R., Whitfield-Gabrieli, S., Scholz, J., & Pelphrey, K. A. (2009). Brain regions for perceiving and reasoning about other people in school-aged children. *Child development*, *80*(4), 1197-1209.

Saxe, R., & Kanwisher, N. (2003). People thinking about thinking people: the role of the temporo-parietal junction in “theory of mind”. Neuroimage, 19(4), 1835-1842.

Saxe, R., & Powell, L. J. (2006). It's the thought that counts: specific brain regions for one component of theory of mind. Psychological science, 17(8), 692-699.

Saxe, R., Brett, M., & Kanwisher, N. (2006). Divide and conquer: a defense of functional localizers. Neuroimage, 30(4), 1088-1096.

Saxe, R., Schulz, L. E., & Jiang, Y. V. (2006). Reading minds versus following rules: Dissociating theory of mind and executive control in the brain. *Social neuroscience*, *1*(3-4), 284-298.

Schmälzle, R., Häcker, F. E., Honey, C. J., & Hasson, U. (2015). Engaged listeners: shared neural processing of powerful political speeches. *Social cognitive and affective neuroscience*, *10*(8), 1137-1143.

Scott, T. L., Gallée, J., & Fedorenko, E. (2017). A new fun and robust version of an fMRI localizer for the frontotemporal language system. *Cognitive neuroscience*, *8*(3), 167-176.

Shahaeian, A., Peterson, C. C., Slaughter, V., & Wellman, H. M. (2011). Culture and the sequence of steps in theory of mind development. *Developmental psychology*, *47*(5), 1239.

Shain, C., Blank, I., Van Shijndel, M., Schuler, W. & Fedorenko, E. (2020). fMRI reveals language-specific predictive coding during naturalistic sentence comprehension. *Neuropsychologia, 138,* 107307.

Silbert, L. J., Honey, C. J., Simony, E., Poeppel, D., & Hasson, U. (2014). Coupled neural systems underlie the production and comprehension of naturalistic narrative speech. *Proceedings of the National Academy of Sciences, 111*(43), E4687-E4696.

Silver, N. C., & Dunlap, W. P. (1987). Averaging correlation coefficients: should Fisher's z transformation be used?. *Journal of Applied Psychology*, *72*(1), 146.

Simon, H. A. (1991). The architecture of complexity. In Facets of systems science (pp. 457-476). Springer, Boston, MA.

Smith, E. A. (2010). Communication and collective action: language and the evolution of human cooperation. *Evolution and human behavior*, *31*(4), 231-245.

Sommerfeld, R. D., Krambeck, H. J., & Milinski, M. (2008). Multiple gossip statements and their effect on reputation and trustworthiness. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1650), 2529-2536.

Sonkusare, S., Breakspear, M., & Guo, C. (2019). Naturalistic stimuli in neuroscience: critically acclaimed. *Trends in cognitive sciences, 23*(8), 699-714.

Sperber, D., & Wilson, D. (1986). *Relevance: Communication and cognition* (Vol. 142). Cambridge, MA: Harvard University Press.

Tager-Flusberg, H., Paul, R., & Lord, C. (2005). Handbook of autism and pervasive developmental disorders, Vol. 1: Diagnosis, development, neurobiology, and behavior.

Tager-Flusberg, H., Paul, R., Lord, C., Volkmar, F., Paul, R., & Klin, A. (2005). Language and communication in autism. *Handbook of autism and pervasive developmental disorders*, *1*, 335-364. –

Tahmasebi, A. M., Davis, M. H., Wild, C. J., Rodd, J. M., Hakyemez, H., Abolmaesumi, P., & Johnsrude, I. S. (2011). Is the link between anatomical structure and function equally strong at all cognitive levels of processing?. *Cerebral Cortex*, *22*(7), 1593-1603.

Theiler, J., Eubank, S., Longtin, A., Galdrikian, B., & Farmer, J. D. (1992). Testing for nonlinearity in time series: the method of surrogate data. *Physica D: Nonlinear Phenomena*, *58*(1-4), 77-94.

Tomasello, M. (2014). The ultra□social animal. *European journal of social psychology*, *44*(3), 187-194.

Tzourio-Mazoyer N, Landeau B, Papathanassiou D, Crivello F, Etard O, Delcroix N, Mazoyer B, Joliot M (2002) Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. Neuroimage 15:273–289.

Varley, R., & Siegal, M. (2000). Evidence for cognition without grammar from causal reasoning and ‘theory of mind’ in an agrammatic aphasic patient. *Current Biology*, *10*(12), 723-726.

Varley, R., Siegal, M., & Want, S. C. (2001). Severe impairment in grammar does not preclude theory of mind. *Neurocase*, *7*(6), 489-493.

Wehbe, L., Blank, I., Shain, C., Futrell, R., Levy, R., Malsburg, T. Smith, N., Gibson, E., Fedorenko, E. (in press). Incremental language comprehension difficulty predicts activity in the language network but not the multiple demand network. *Cerebral Cortex*.

Willems, R. M., Nastase, S. A., & Milivojevic, B. (2020). Narratives for neuroscience. *Trends in neurosciences*, *43*(5), 271-273.

Whitfield-Gabrieli, S., & Nieto-Castanon, A. (2012). Conn: a functional connectivity toolbox for correlated and anticorrelated brain networks. *Brain connectivity*, *2*(3), 125-141.

Wiesmann, C. G., Schreiber, J., Singer, T., Steinbeis, N., & Friederici, A. D. (2017). White matter maturation is associated with the emergence of Theory of Mind in early childhood. *Nature communications, 8*, 14692.

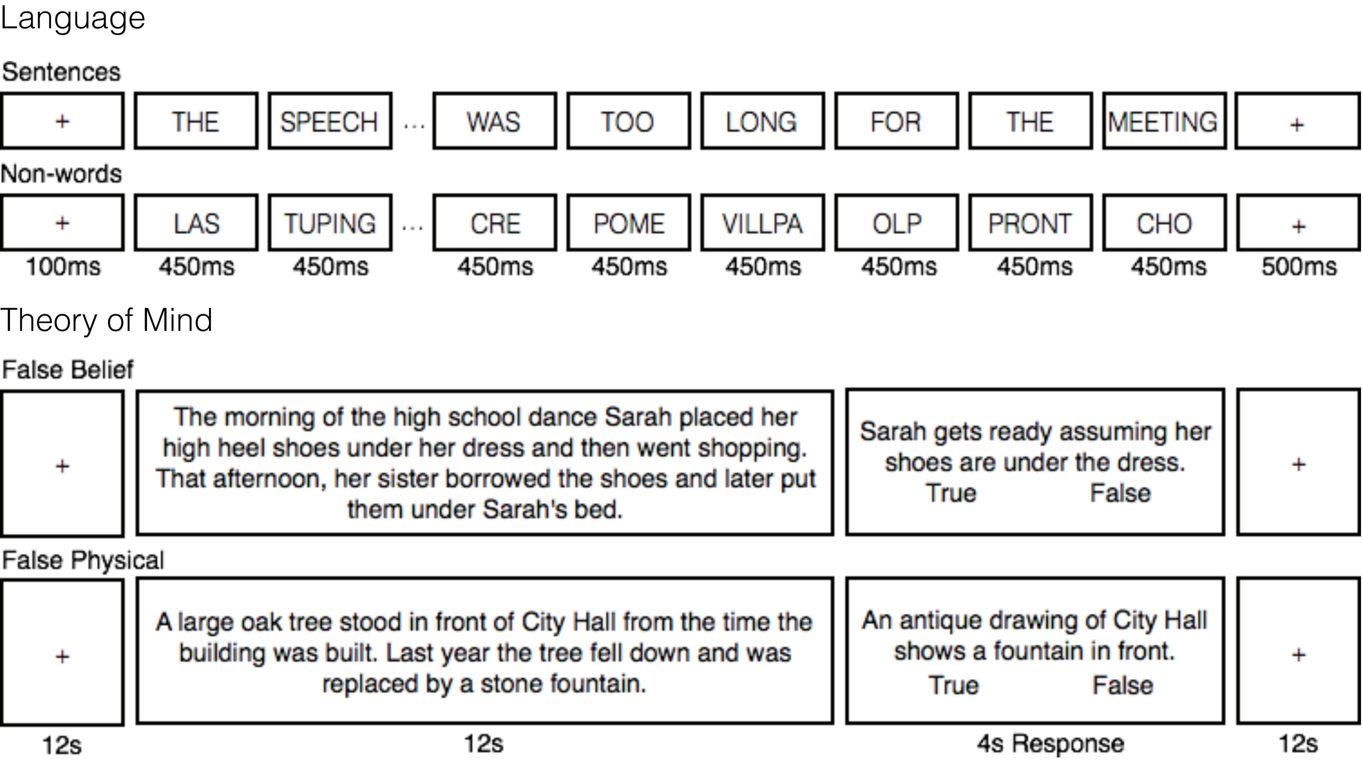
Wilkinson, K. M. (1998). Profiles of language and communication skills in autism. *Mental Retardation and Developmental Disabilities Research Reviews*, *4*(2), 73-79.

Willems, R. M., Benn, Y., Hagoort, P., Toni, I., & Varley, R. (2011). Communicating without a functioning language system: implications for the role of language in mentalizing. *Neuropsychologia*, *49*(11), 3130-3135.

Willems, R. M., Van der Haegen, L., Fisher, S. E., & Francks, C. (2014). On the other hand: including left-handers in cognitive neuroscience and neurogenetics. *Nature Reviews Neuroscience*, *15*(3), 193.

Wilson, S. M., Molnar-Szakacs, I., & Iacoboni, M. (2007). Beyond superior temporal cortex: intersubject correlations in narrative speech comprehension. *Cerebral cortex*, *18*(1), 230-242.

Wimmer, H., & Perner, J. (1983). Beliefs about beliefs: Representation and constraining function of wrong beliefs in young children's understanding of deception. *Cognition*, *13*(1), 103-128.



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.

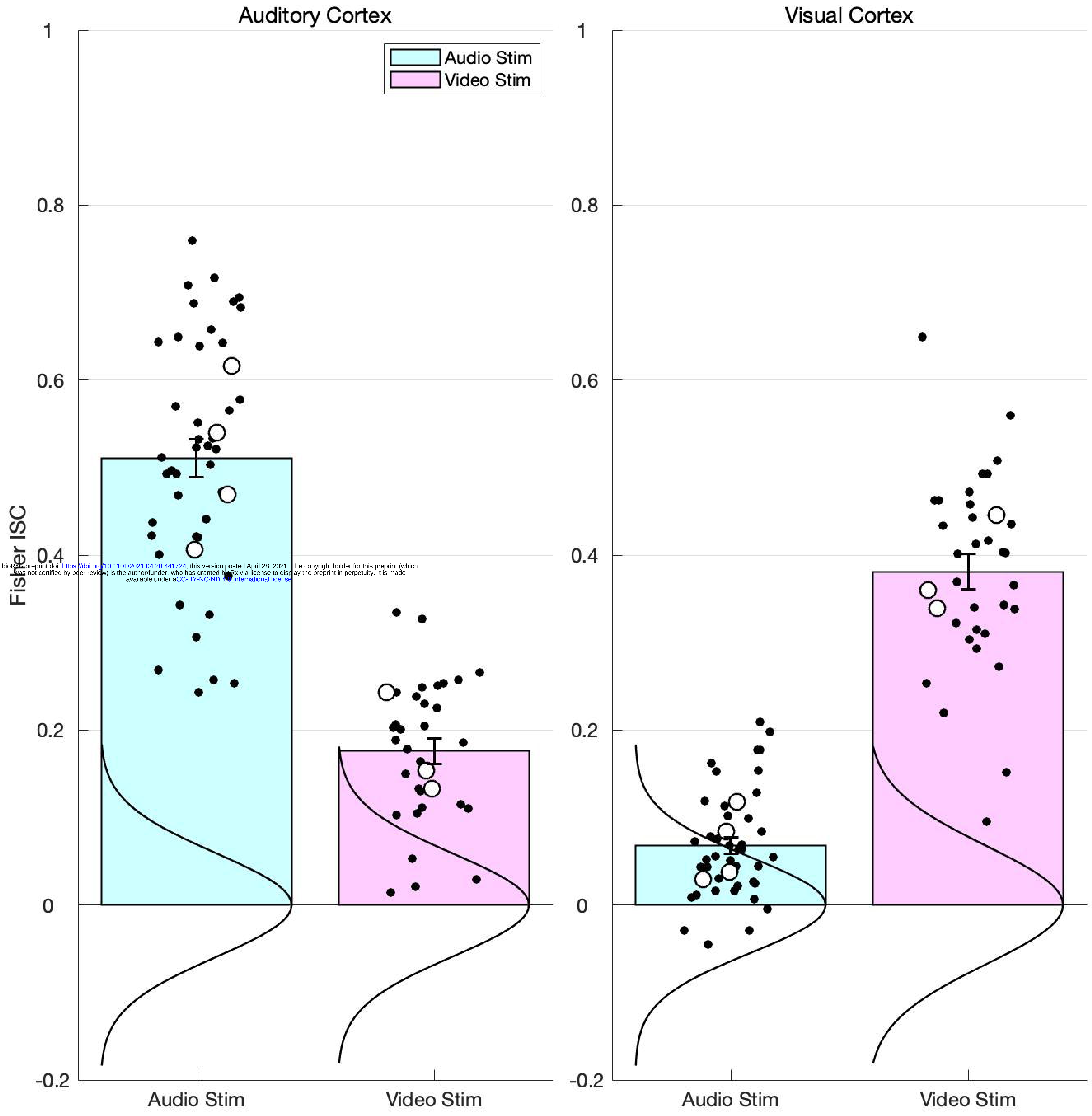
Sarah gets ready assuming her shoes are under the dress.

True False

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


Auditory Cortex
Visual Cortex
Audio Stim
Video Stim
Fisher ISC
1
0.8
0.6
0.4
0.2
0
-0.2
1
0.8
0.6
0.4
0.2
0
-0.2
Audio Stim
Video Stim
Audio Stim
Video Stim


Language masks
MFG
IFG
IFGorb
AntTemp
PostTemp
Condition Type: Language network
🟧 +Lang+ToM
🟩 -Lang+ToM
🟥 +Lang-ToM
Fisher ISC
1
0.8
0.6
0.4
0.2
0
-0.2
+Lang+ToM
-Lang+ToM
+Lang-ToM
Condition: Language network
Story
AudioPlay
Dialog
AnimShort
SilentFilm
IntentShapes
ExpoText


ToM masks
TPJ
PC
DMPFC
Condition Type: ToM network
🟧 +Lang+ToM
🟩 -Lang+ToM
🟥 +Lang-ToM
Fisher ISC
1
0.8
0.6
0.4
0.2
0
-0.2
+Lang+ToM
-Lang+ToM
+Lang-ToM
Condition: ToM network
Story
AudioPlay
Dialog
AnimShort
SilentFilm
IntentShapes
ExpoText