Understanding jokes relies on the Theory of Mind system

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Abstract

To communicate successfully, we often go beyond literal meaning: we make sarcastic remarks, ask others for favors, and engage in face-saving acts. Do these abilities rely on the same mechanisms as literal sentence interpretation? Or does pragmatic reasoning draw on general social-cognitive abilities? Using a functional localization fMRI approach, we examined activity in i) the language system, ii) the Theory-of-Mind (ToM) system, and iii) the domain-general "multiple demand" system, sensitive to diverse demanding tasks, while participants processed one-liner-style jokes and non-joke controls. Only the ToM system was robustly sensitive to jokes. Further, funnier stimuli (as judged by the participants) elicited stronger responses, and the size of the jokes>non-jokes effect in ToM regions across individuals was predictive of how funny they found the jokes. Thus 'getting' jokes – and perhaps pragmatic processing more broadly – appears to stem from the same cognitive abilities that allow us to imagine what another person is thinking.

Introduction

Human language is a critical part of our social toolbox, and it functions within social contexts that can radically alter the meaning of an utterance (e.g., Grice, 1975; Lakoff & Johnson, 2003). "He's good at sharpening pencils" may be a reasonably positive description of a kindergartener, but as a response to the question "Is Bob a good candidate to chair that committee?" implies a negative evaluation of Bob, the committee, or both. Going beyond the literal meaning of an utterance allows us to subtly – or not so subtly – express our attitudes about the world using irony and sarcasm, joke about things, flirt, ask people to do things for us in polite ways, tell white lies, and more generally avoid confrontation. Are these pragmatic abilities supported by the same cognitive and brain mechanisms as the literal interpretation of the linguistic signal? Or does pragmatic reasoning draw on more general social-cognitive abilities? We here examine the division of labor between the core language processing mechanisms and mechanisms that support social cognition by examining a particular test case of social language: jokes.

Investigations of individuals with developmental and acquired disorders have suggested that basic language comprehension is dissociable from social/pragmatic reasoning. For example, individuals with severe aphasia exhibit impairments with many aspects of language and yet preserve the ability to reason about others' mental states (Apperly et al. 2006; Varley & Siegal, 2000). On the other hand, some individuals with autism spectrum disorders appear to have intact language processing abilities while experiencing difficulties with social reasoning (e.g., Joseph et al. 2002). Consistent with this dissociation in behavior, brain-imaging investigations have identified distinct sets of brain regions for language interpretation and social reasoning. In particular, language interpretation – including lexical, syntactic, and compositional semantic processing – recruits a left-lateralized fronto-temporal network (Binder, 1997; Fedorenko et al., 2010), whereas social cognition, including Theory of Mind reasoning (i.e., thinking about mental states of others), recruits a network composed of midline cortical regions as well as bilateral regions at the junction of temporal and parietal lobes (Fletcher, 1995; Saxe & Kanwisher, 2003).

However, apart from revealing this dissociation between the mechanisms that support core linguistic interpretation and those that support social cognition, prior literature has not provided a clear answer to the question of whether pragmatic reasoning recruits primarily the former, primarily the latter, or both systems (or some additional set of brain regions). fMRI investigations of non-literal/pragmatic processing have reported activations in diverse cortical brain regions. For example, a recent meta-analysis of fMRI studies of humor processing (Vrtička, Sander, & Vuilleumier, 2013) has reported activation peaks all over the association cortices across both hemispheres. Investigations of patients with acquired brain damage have implicated the RH (Eisenson, 1962; Myers, 1999), but though these studies suggest that this damage may be sufficient to disrupt pragmatic processing (and thus that the core LH language network is not sufficient for these abilities) they leave open the question of *which mechanisms in the right hemisphere are critical*. We use fMRI to examine three systems housed in the RH: i) the right homologs of the left-hemisphere language regions, ii) the system that supports social cognition, whose most selective component resides in the RH at the junction of temporal and parietal lobes (the right temporo-parietal junction, rTPJ, Saxe & Powell, 2006), and iii) the fronto-parietal domain-general "multiple demand (MD)" system (e.g., Duncan, 2010), implicated in executive functions. The latter is included because general attention, working memory, and cognitive control abilities have been argued to be important for pragmatic reasoning (e.g., Brown-Schmidt, 2009; Martin & McDonald, 2003).

In our critical task, participants read sentences like the following (all stimuli from Coulson & Williams, 2005):

(1a) She went on a fourteen-day diet, but all she lost was two weeks.

Appreciating the humor in the joke requires appreciating that the sentence implies that she did *not* lose any weight, that people usually intend to lose weight on a diet, that losing time is an additional negative, and so on. To create a non-humorous control sentence, the joke is modified with a single word that removes the need to make these inferences to understand the meaning:

(1b) She went on a fourteen-day diet, but all she lost was two ounces.

Given that i) high-level cortical regions are highly variable in their precise locations across individuals, and ii) distinct functional sub-regions often lie in close proximity to one another within the same macroanatomical areas (Deen et al., 2015; Fedorenko, Nieto-Castañon, & Kanwisher, 2012; Scholz et al., 2009), we functionally define each target set of regions in each individual participant; these regions' responses are then examined to the critical pragmatic task (joke comprehension, in this study).

In the language localizer task (Fig. 1a), participants read sentences and lists of pronounceable nonwords in a blocked design. The Sentences>Nonwords contrast targets brain regions sensitive to high-level linguistic processing (Fedorenko et al., 2010). In the Multiple Demand system localizer task (Fig. 1b), participants performed a spatial working memory task that we have previously found to activate the MD system broadly and robustly (Fedorenko, Duncan, & Kanwisher, 2013). On each trial, participants had to keep track of four (easy condition) or eight (hard condition) locations in a 3 x 4 grid (Fedorenko, Behr, & Kanwisher, 2011). The Hard>Easy contrast targets brain regions engaged in cognitively demanding tasks (Duncan & Owen, 2000). Finally, in the Theory of Mind localizer task, participants read false belief stories, which have been used for decades in behavioral settings (Wimmer & Perner, 1983), and narratives that do not involve thinking about another person's thoughts. These controls instead involve holding multiple representations (e.g., photographs) rather than mental states in mind (see Fig. 1c). The False belief>False photograph contrast targets brain regions engaged in thinking about another person's thoughts and beliefs (Dufour et al., 2013; Saxe & Kanwisher, 2003). This *functional localization* approach affords stronger inferences about the reliance of pragmatic reasoning on the three target systems compared to inferences made based on approximate anatomical locations of activations for a pragmatic task (see e.g., Poldrack, 2011 for discussion). This approach can thus shed light on the actual cognitive mechanisms that support the processing of jokes.

Methods

Participants

Twelve adults (aged 19-46, mean age 24.3; 9 female) – MIT students and members of the Cambridge community – were paid for participating in 2-hour scanning sessions. The sample size was determined based on Fedorenko's prior experience with functional-localization-based fMRI studies, for which samples of 10-14 are typical (Blank et al., 2014; Fedorenko et al., 2010). All were native speakers of English, naïve to the purposes of the study with normal hearing and vision, and no history of neurological or linguistic impairment. One participant was left-handed but showed typical left-lateralized language activations. Participants gave informed consent following MIT's Committee on the use of Humans as Experimental Subjects.

Design, materials and procedure

Each participant performed the target joke comprehension experiment and three "localizer" tasks described below (Figure 1). Our approach thus involves two stages: First, we use the localizers to identify three sets of functional regions of interest (fROIs) in each participant, and then, in the critical task, test how those fROIs respond to Joke stimuli vs. matched Non-joke controls.

Language localizer: Participants read sentences and nonword lists in a blocked design. Each trial started with 100ms pre-trial fixation, followed by a 12-word-long sentence or a list of 12 nonwords presented one at a time at the rate of 450ms per word/nonword. Then, a line drawing of a hand pressing a button appeared for 400ms (participants were instructed to press a button whenever they saw this icon), and finally a blank screen was shown for 100ms, for a total trial duration of 6 seconds. The button-pressing task was included to help participants stay alert and focused. Each block consisted of 3 trials and lasted 18s. Each run consisted of 16 experimental blocks (8 per condition), and five fixation blocks (14s in duration each), for a total duration of 358s (5min 58s). Each participant performed two runs. Condition order was counterbalanced across runs.

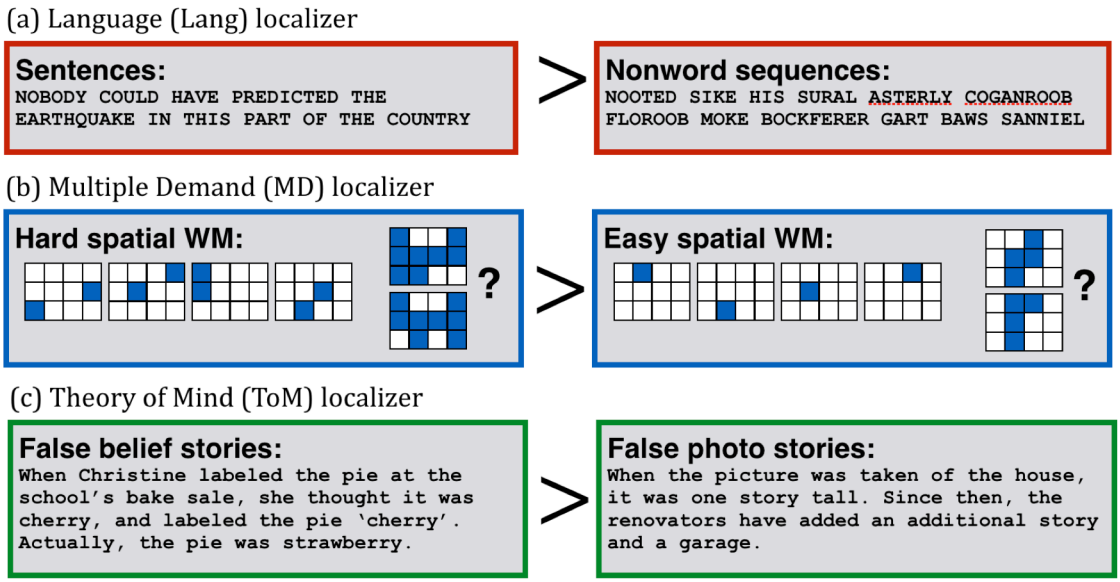


Figure 1: Localizer tasks administered to participants in the Joke Comprehension study.

Multiple Demand localizer: Participants performed a spatial working memory task in a blocked design. A series of locations appeared within a 3x4 grid, and then participants performed a two-alternative, forced-choice task at the end of each trial to indicate the set of locations that they just saw. Each trial lasted 8s (see Fedorenko et al., 2011, for details). Each block consisted of 4 trials and lasted 32s. Each run consisted of 12 experimental blocks (6 per condition), and 4 fixation blocks (16s in duration each), for a total duration of 448s (7min 28s). Each participant performed one run.

Theory of Mind localizer: Participants read stories about false beliefs and control stories. Each story (trial) was presented for 10s, and then a true/false question about the content of the story was displayed for 4s, followed by 12s of rest. Each run consisted of 10 experimental trials (5 per condition), and 11 fixation blocks (12s at the beginning of the run and 12s after every trial), for a total duration of 272s (4min 32s). Each participant performed 1 or 2 runs. Condition order was counterbalanced across runs when participants performed two runs.

Joke Comprehension task: We used 156 items (78 per condition), developed by Coulson & Williams (2005), consisting of a joke and a non-joke control with a single word replaced (see (1); see Supplemental materials for a complete list). In (1), a high-probability completion would be *two pounds*; the stimuli instead use two relatively low-probability completions, *two weeks* and *two ounces*. Thus, the critical word in both conditions was somewhat surprising, but only in the joke condition did it require a humorous reinterpretation.

In an event-related design, participants read the sentences (presented all at once) and rated each sentence for how funny it was. Trials were 8s long, beginning with 250ms of fixation followed by the joke/non-joke sentence presented for 5.75s, and then the rating question presented for 2s. Participants responded to the rating question by pressing a button on a button box numbered 1–4 to indicate how funny they though each sentence was (1= Not at all funny, 4= Very funny). Reaction times were recorded as a measure of basic processing difficulty. This task served to keep participants engaged, and also allowed us to carry out analyses based on individual funny-ness ratings.

Each run lasted 532s (8min, 52s) and included 26 8s trials per condition and 116s of fixation interleaved among the trials (between 0 and 14s between each pair of trials). The condition orders and timings were created using the optseq algorithm (Dale, 1999). Each participant saw at least 2 runs (52 trials total per condition); three participants saw an additional run for a total of 78 trials per condition; condition orders were counterbalanced across runs and participants.

fMRI data acquisition and preprocessing

Structural and functional data were collected on the 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 128 axial slices with 1mm isotropic voxels (TR=253ms, TE=3.48ms). 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), with the following acquisition parameters: thirty-one 4mm thick near-axial slices, acquired in an interleaved order with a 10% distance factor; 2.1mm x 2.1mm in-plane resolution; field of view of 200mm in the phase encoding anterior to posterior (A>P) direction; matrix size of 96mm x 96 mm; TR of 2000ms and TE of 30ms. Prospective acquisition correction was used to adjust the positions of the gradients based on the participant's motion one TR back. The first 10s of each run were excluded to allow for steady-state magnetization.

MRI data were analyzed using SPM5 and custom MATLAB scripts. Each participant's data were motion corrected and then normalized into a common brain space (the Montreal Neurological Institute (MNI) Brain Template) and resampled into 2mm isotropic voxels. The data were then smoothed with a 4mm Gaussian filter and high-pass filtered (at 200s). The localizer tasks' and critical task's effects were estimated using a General Linear Model in which each experimental condition was modeled with a boxcar function – modeling the entire block or event – convolved with the canonical hemodynamic response function.

Definition of group-constrained, subject-specific fROIs

In the group-constrained subject-specific (GSS) approach, developed by Fedorenko et al. (2010), a search space or "parcel" corresponding to a brain area where most subjects have been shown in prior work to exhibit activity for the relevant contrast is intersected with each individual participant's activation map for the same contrast, and a subset of voxels within each parcel showing the strongest effect (individual functional regions of interest, fROIs) is selected for further analysis. In particular, we chose 10% of voxels based on the *t*-values within each parcel. Three sets of fROIs were defined (Fig. 1): high-level language processing fROIs that selectively support language processing (Fedorenko et al., 2011; Monti & Osherson, 2012) and their right-hemisphere homologues, ToM fROIs that support mentalizing (e.g., Saxe & Kanwisher, 2003), and multiple demand (MD) fROIs that respond to diverse demanding cognitive

tasks and exhibit sensitivity to effort (Duncan, 2010; Fedorenko et al., 2013). Within these individually-defined fROIs, we tested the response to the Jokes and Non-jokes conditions. These analyses were complemented with a traditional whole-brain random-effects analysis (see Supplemental materials).

For the language and the ToM networks, parcels were derived from group-level representations of localizer data from previous studies. To define the language fROIs, we used six parcels (Fig. 3) derived from a probabilistic activation overlap map for the Sentences>Nonwords contrast based on data from 220 participants. These parcels included three regions in the left frontal cortex: two in the inferior frontal gyrus (LIFG and LIFGorb), and one in the middle frontal gyrus (LMFG), and three regions in the left temporal and parietal cortices (LAntTemp, LPostTemp, and LAngG). These parcels are similar to the parcels reported in Fedorenko et al. (2010) based on a set of 25 participants, except that the two anterior temporal parcels (LAntTemp, and LMidAntTemp) and two posterior temporal parcels (LMidPostTemp and LPostTemp) are respectively grouped together. To define the ToM fROIs, we used seven parcels (Fig. 3) derived from a group-level representation of data for the False belief>False photograph contrast based on data from 462 participants (Dufour et al., 2013). These parcels included regions in the temporo-parietal junction bilaterally (RTPJ and LTPJ), four midline cortical regions (three in the medial prefrontal cortex, DMPFC, MMPFC, and VMPC, and one in the precuneus, PC), and a region in the right STS. For the MD network, we used a set of eighteen anatomical parcels from the Tzourio-Mazoyer et al.'s (2002) atlas, following Fedorenko et al. (2013). All parcels are available for download from http://web.mit.edu/evelina9/www/funcloc.html., and all group analyses (as well as materials for the presentation script) are available at https://github.com/mekline/Jokes-Analysis.

Percent signal change values for the localizer and critical conditions were extracted from each fROI (for the former, an across-runs cross-validation was used; Nieto-Castanon & Fedorenko, 2012), and statistical tests across participants were then performed on these values for each system, using standard Student's *t*-tests and linear mixed-effects models.

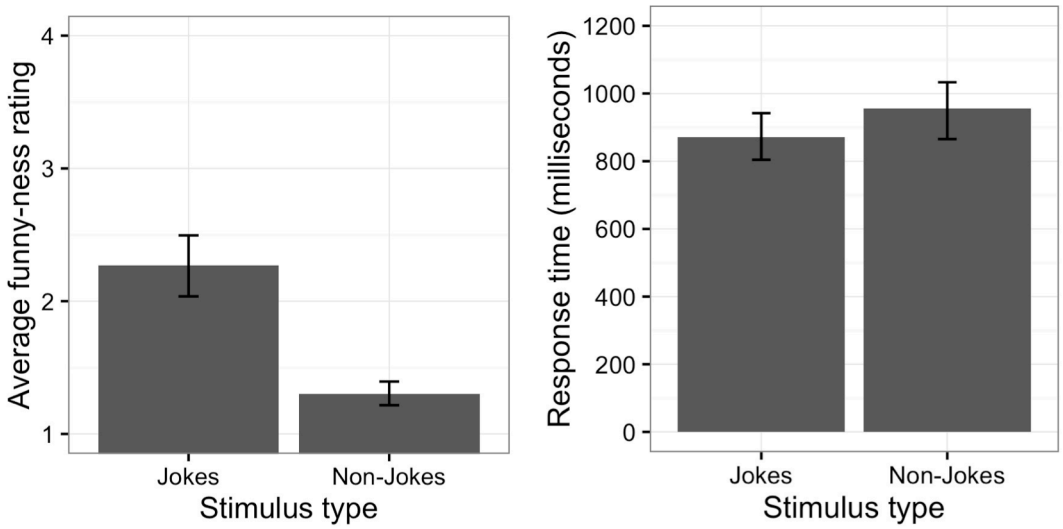


Figure 2: Behavioral ratings and response times to the critical Jokes/Non-Jokes comprehension task ("How funny was the sentence you just read? 1 = Not at all funny, 4 = Very funny.") Error bars in all bar graphs represent bootstrapped 95% confidence intervals by participant.

Results

Behavioral Responses

As shown in Figure 2, participants rated Jokes as funnier than Non-jokes ($t=7.43$, $p<0.001$). Reaction times did not differ between conditions ($t=-1.44$, $p=0.16$).

Neural Responses

Before we examined the responses of each set of fROIs to the critical Joke and Non-joke conditions, we assessed the localizer data quality to ensure that the fROIs behaved as expected. To do so, we calculated the percent signal changes to the respective localizer conditions, using an across-runs cross-validation procedure (e.g., Nieto-Castañón & Fedorenko, 2012) to maintain independence of voxel selection and response estimation All fROIs showed significant responses to their respective contrast (see Supplemental), with the sole exception of the VMPFC ToM fROI, which was consequently excluded from the critical analyses.

To test whether the processing of jokes elicits a stronger response in any of the three systems, we then examined the responses of each set of fROIs to the Joke and Non-joke conditions. We report each system with t tests at the fROI level as well as a linear mixed effects model for the whole system, and report effect size as the mean signal change between the critical jokes and non-jokes conditions. We did not expect the LH language fROIs to be sensitive to the Jokes>Non-jokes contrast given prior findings from individuals with severe aphasia who nevertheless preserve the ability for pragmatic/social reasoning (e.g., Varley & Siegal, 2000). However, we expected that some combination of right-hemisphere language fROIs, ToM fROIs, or MD fROIs would respond to this contrast, giving us insight into the kinds of mental processes that may be engaged in understanding the humor in a joke.

(1) Language network

Right-hemisphere language network

All fROIs responded robustly to both Jokes and Non-jokes stimuli relative to the fixation baseline ($ts>3.76$, $ps<0.0016$; see Supplemental for tables showing stats for all the individual fROIs), except for the right AngG fROI, which did not respond significantly above fixation to either condition ($ts<1$, $ps>0.25$). These above-baseline responses are to be expected given that the critical materials were verbal in nature, and many prior studies have reported reliable, albeit weaker than in the LH, responses to linguistic materials in the RH language regions (e.g., Blank et al., 2016). Critically, however, responses did not differ between conditions in any region ($ts<1.69$, $ps>0.059$), and a linear mixed effects model showed no reliable effect of condition ($\chi^2=0.48$, $p>0.25$). The difference (jokes-non jokes) in mean signal change across all fROIs was 0.037%.

Left-hemisphere language network

The LH language fROIs also did not differentiate between the two conditions ($ts<1.75$, $ps>0.054$), except for the left AngG fROI ($t=3.27$, $p=0.004$), although all regions showed robust responses to both conditions relative to the fixation baseline ($ts>3.02$, $ps<0.006$). A linear mixed effects model showed no reliable effect of condition ($\chi^2=0.21$, $p>0.25$). The difference in mean signal change was 0.041%.

(2) Multiple demand (MD) network

Right-hemisphere MD network

Some of the RH MD fROIs showed above-baseline responses to both Joke and Non-joke stimuli, although these responses were generally weaker than the responses in the language fROIs. Only one region – the RParInf fROI – responded reliably more strongly during the processing of Jokes compared to Non-jokes ($t=2.56$, $p=0.013$); all other fROIs did not reliably differentiate between the two conditions ($ts<1.28$, $ps>0.113$). Further, there was no effect of condition by a linear mixed effects analysis ($\chi^2=0.58$, $p>0.25$). The difference in mean signal change was 0.036%.

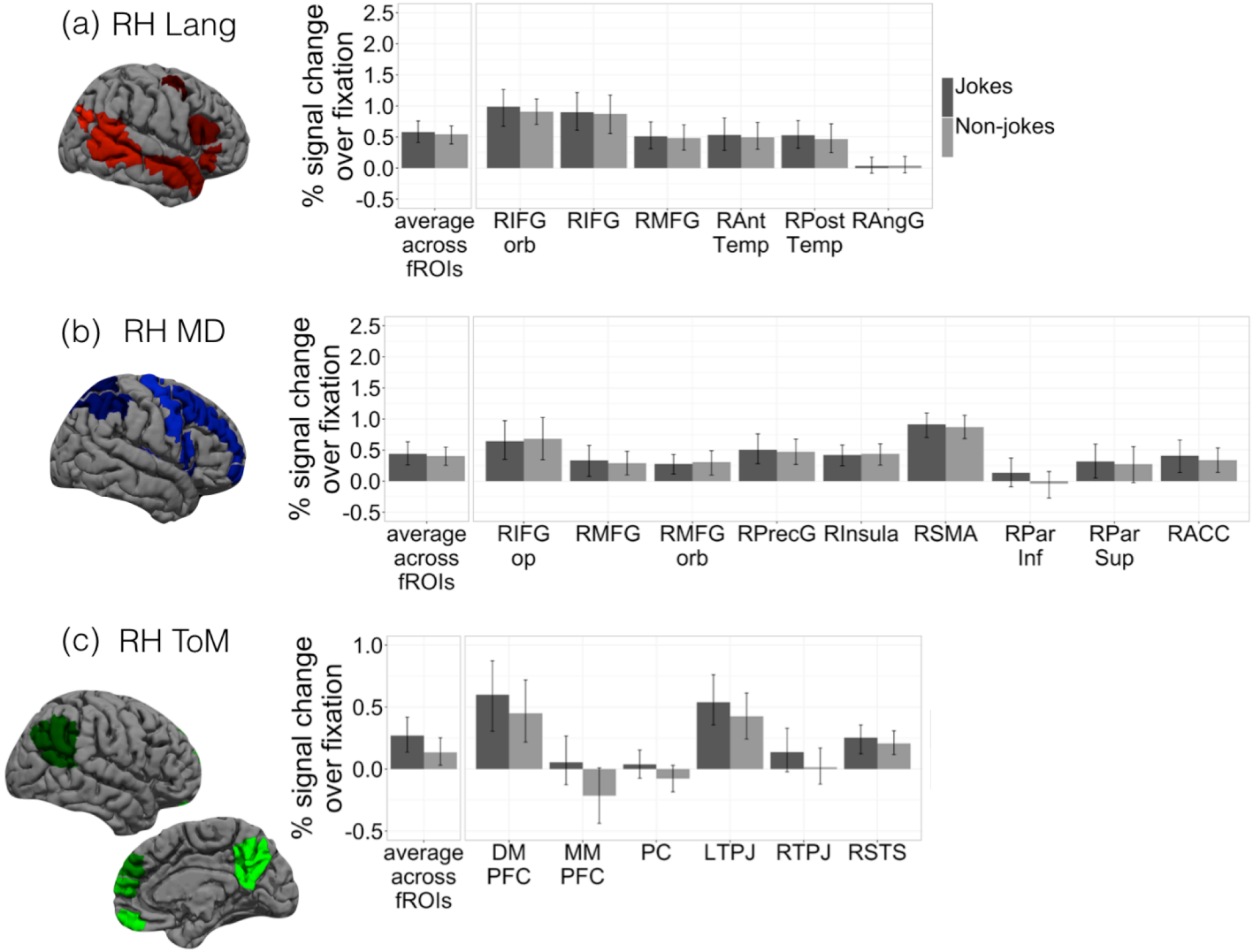
Left-hemisphere MD network

Overall, the response to both types of stimuli was higher than in the RH MD regions, and quite a few of the LH MD fROIs responded reliably more strongly during the processing of Jokes compared to Non-jokes. These fROIs included: LIFGop, LPrecG, LInsula, LParInf, and LParSup ($ts>2.04$, $ps<0.033$). A linear mixed effects model showed a marginal effect of condition ($\chi^2=3.47$, $p=0.063$). The difference in mean signal change was 0.119%.

(3) Theory of Mind (ToM) Network

In contrast to the language and MD fROIs in the RH, most ToM fROIs responded reliably more strongly during the processing of Jokes than Non-jokes, including the component most functionally selective for mental state attribution (Saxe & Powell, 2006): the RTPJ fROI ($t=2.72$, $p=0.010$), but also the LTPJ fROI ($t=3.36$, $p=0.003$), the MMPFC fROI ($t=3.95$, $p=0.001$), and the PC fROI ($t=2.75$, $p=0.009$). Considering the system as a whole, a linear mixed effects model showed a highly reliable effect of condition, with the Jokes condition eliciting a stronger response than the Non-jokes condition ($\chi^2=6.65$, $p=0.010$). The difference in mean signal change was 0.136%.

Figure 3 (Neural responses in the right hemisphere): The parcels – used to constrain the definition of individual fROIs – and the responses to the Joke and Non-joke conditions in the (a) Language, (b) Multiple demand, and (c) Theory of Mind fROIs (VMPFC not plotted, see localizer results). Each graph shows the average signal change above fixation for the two conditions across all fROIs, followed by responses in each fROI individually. Error bars indicate 95% confidence intervals by participants.



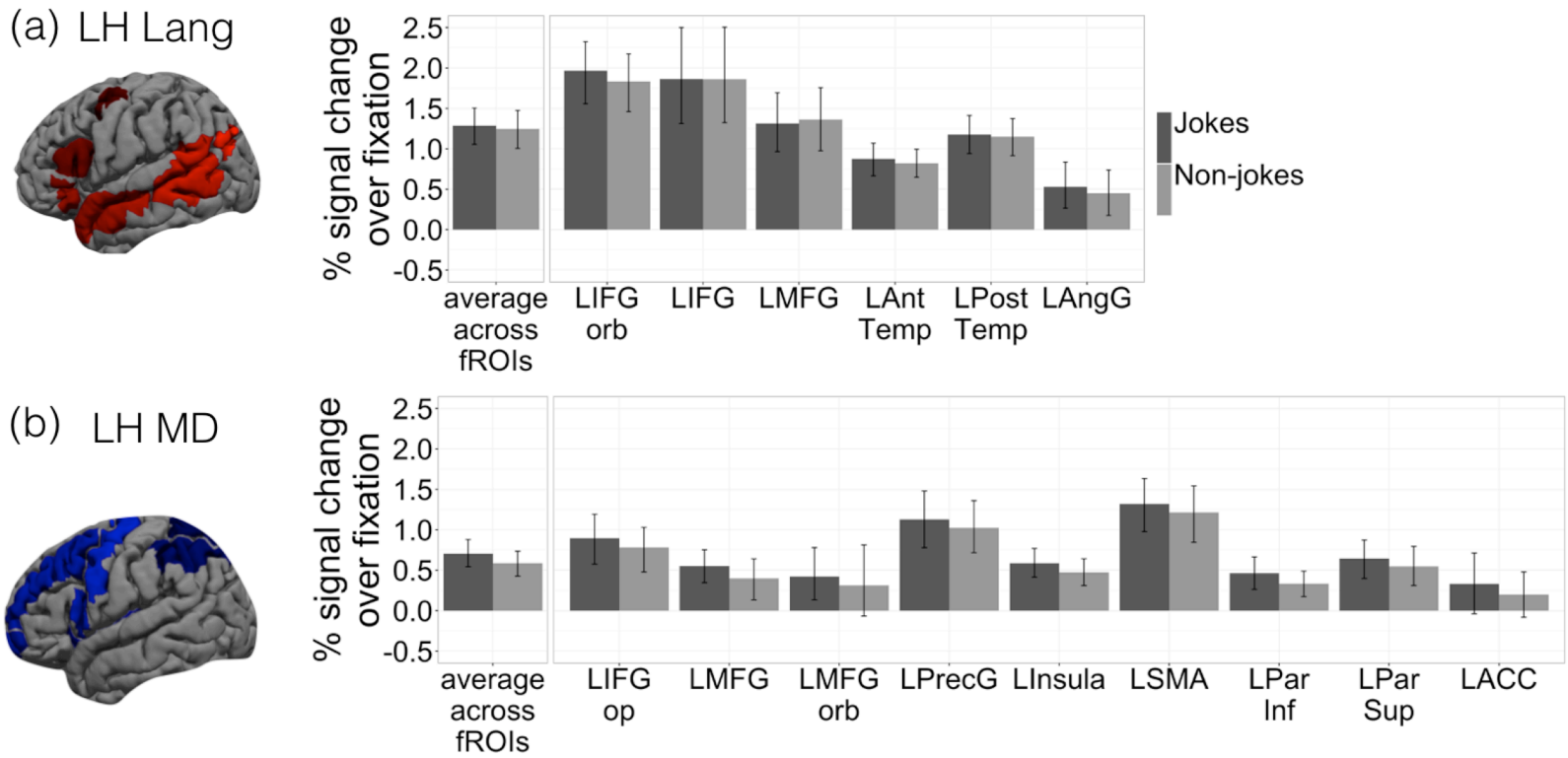


Figure 3, continued (Neural responses in the left hemisphere)

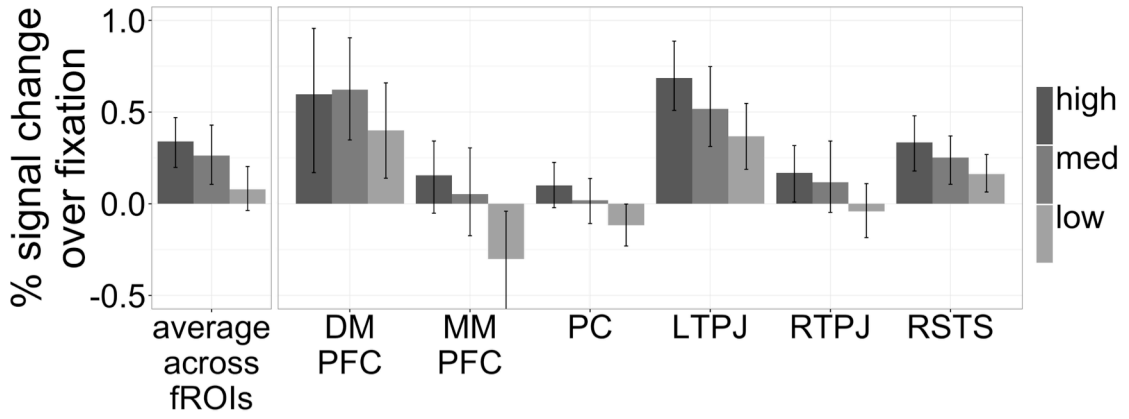


Figure 4: Responses in the ToM fROIs to the Jokes task, with trials coded by individual 'funny-ness' ratings for each participant individually. (VMPFC not included, see localizer results)

To characterize the responses in the ToM system in greater detail, we performed two additional analyses. First, we re-modeled the fMRI responses with individual participants' funny-ness ratings (see Behavioral results). For each participant, each trial was coded as funny (if it got a response of 3 or 4), somewhat funny (if it got a response of 2), and not funny (if it got a response of 1). Trials that did not get a response were coded as a fourth conditions and not examined further. While sacrificing the close linguistic matching between the Joke and Non-joke sentence in each pair, this analysis is sensitive to a) individual differences in the subjective experience of humor for any given sentence, and b) inter-item differences in how funny they were. A clear parametric pattern – with funnier sentences resulting in higher responses – was observed across all fROIs (ts>2.84, ps<0.001; Fig. 4), except the DMPFC fROI (t=1.32, p=0.107). This pattern was also reliable by a linear mixed

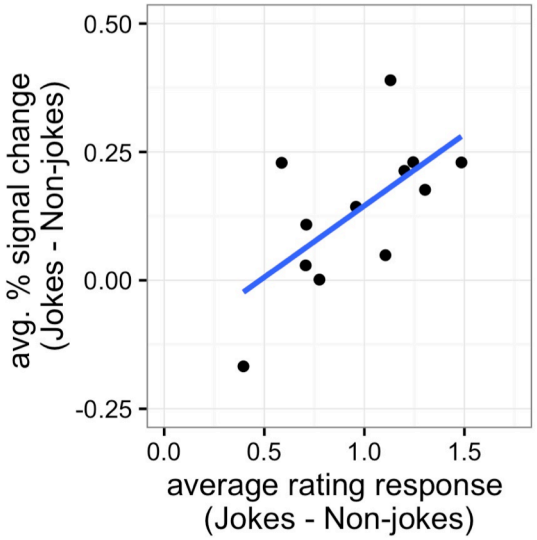


Figure 5: Correlation between individual behavioral ratings of Jokes vs. Non-Jokes and signal change in ToM regions to the same stimuli.

effects model treating funny-ness rating as an ordinal factor (χ^2=11.40, p=0.003). Finally, we examined whether the degree to which any given individual found the Joke stimuli to be funny (compared to the Non-joke control) predicted the size of the Jokes>Non-Jokes effect (averaged across the ToM fROIs). To do so, we fit a regression model[1], finding a significant relationship (F=6.89, p=0.025; see Figure 5).

(3) Comparison between systems

To support the analyses above, we directly compared the Joke>Non-joke contrast between the ToM fROIs and each of the language and MD sets of fROIs, in the RH and LH. The effect was significantly larger in the ToM fROIs than the RH language fROIs (χ^2=5.11, p=0.032), and RH MD fROIs (χ^2=4.62, p=0.03), but it was not significantly different from the LH language fROIs (χ^2=2.32, p=0.12) or the LH MD fROIs (χ^2=0.26 p>0.25), in line with the fact that several LH MD fROIs, and the LAngG language fROI responded more strongly to Jokes than Non-jokes.

Discussion

In contrast to most previous research on the neural correlates of humor, or, more generally, pragmatic processing, we adopted an approach where we targeted three neural networks whose activity has been strongly linked with particular cognitive processes: i) the fronto-temporal language system linked to high-level language processing (e.g., Fedorenko et al., 2011), ii) the fronto-parietal multiple demand (MD) system linked to executive functions (e.g., Duncan, 2010) and iii) the Theory of Mind (ToM) system linked to social-cognitive reasoning, including mentalizing (e.g., Gallagher & Frith, 2003; Saxe & Kanwisher, 2003; Moriguchi et al., 2006). We found the ToM system to be robustly sensitive to humor processing, exhibiting stronger responses to jokes compared to minimally different non-joke controls. In addition, we observed some sensitivity to humor processing in the LH component of the domain-general MD system and in one LH language fROI (the LAngG fROI).

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[1] Model specification `lm(meanSigChange ~ meanResponseChange)`; no random slopes present because each participant contributes a single observation.

These findings support the view that 'getting' jokes – and perhaps pragmatic processing more broadly – stems from the same basic cognitive abilities that allow us to imagine what another person is thinking (see e.g., Martin & McDonald, 2003). Activation in the RTPJ is especially notable because of this fROI's selective engagement in understanding others' mental states (e.g., Saxe & Powell, 2006). In this study, the speaker's/writer's intent may become clear when the 'punchline' word is read. These results also suggest that the pragmatic deficits that often follow damage to the right hemisphere may result from damage to some parts of the ToM system (specifically, the rTPJ and/or the RSTS) rather than RH homologues of the language regions, or the right-hemisphere components of the domain-general MD system. Thus, ToM-related processes play a specific and central role in at least some aspects of pragmatic reasoning.

Clearly, understanding "one-liners" like the jokes in this study requires engagement of the language system: you will not be able to understand the joke if you cannot understand the words and how they combine together to form meaning. However, importantly, this kind of linguistic impairment would leave you unable to understand *any* linguistic utterances, not jokes specifically, in line with similarly strong responses to both joke and non-joke conditions in the LH and RH homologous language regions, with the exception of the LAngGfROI. Furthermore, prior evidence from severe aphasia suggests that non-linguistic pragmatic/social abilities appear to be largely preserved following (even extensive) damage to the LH language regions (e.g., Apperly et al., 2006; Varley & Siegal, 2000). Thus, although the LH language system is critical for basic literal interpretation of linguistic signals, it does not appear to be at the core of pragmatic reasoning. The small but reliable effect in the LAngG language fROI is interesting and in line with prior work showing that this fROI dissociates from the rest of the LH language fROIs in diverse functional correlation measures (e.g., Chai et al. 2012). The relationship between this language fROI and the ToM system, and understanding of the division of labor between them during pragmatic processing is an important avenue for future work.

Some contribution from the domain-general executive resources (attention, working memory or cognitive

control) may be necessary for understanding jokes, and perhaps for making other kinds of pragmatic inferences, as evidenced by stronger responses to the joke condition in the left hemisphere MD regions. Indeed, some prior work on patients with brain damage has suggested a role for the executive system in pragmatic/social reasoning (cf. Mikola, 2010). Ultimately, a complete account of pragmatic processing will need not just to determine which brain systems – and the corresponding sets of mental processes – are engaged, but to explain how these different kinds of computations are orchestrated in a dynamic fashion during linguistic exchanges, including an understanding of what kind of information may be exchanged between the different systems.

Do other pragmatic phenomena also recruit the Theory of Mind system? Some prior work suggests that this indeed may be the case. For example, Spotorno and colleagues (2012) observed activity in the ToM network when a sentence was ironic in context (e.g., "We gave a marvelous performance!" after a disappointing concert) compared to when it could be interpreted literally. Similarly, van Ackeren et al. (2012) reported ToM activity for indirect requests. However, the term "pragmatics" is currently used in the literature broadly, to refer to diverse phenomena, from understanding quantifiers like *some*, to resolving reference, to parsing politeness registers, to navigating complex social interactions in conversation. Even within a particular phenomenon there can be substantial variability. For example, verbal humor includes things like puns, mixed metaphors, one-liner jokes like those used here, and jokes that require long elaborate contexts, among many others (e.g., Dynel, 2009). A long-term goal of this line of research is to "carve pragmatics at its joints" (cf. Plato, *Phaedrus* 265e), identifying natural classes of phenomena and abilities that together comprise a coherent account of the cognitive operations involved in complex communication. This will plausibly require characterizing the contributions of each of the three systems examined here to diverse pragmatic phenomena and drawing on complementary methods that would jointly allow us to understand which brain regions (linked to particular cognitive processes) are active at which times during pragmatic reasoning, and which of these regions are causally important. A deeper understanding of neural activity related to pragmatic reasoning, including its time-course and

causal nature, can guide us toward richer, and more grounded, models of how we achieve communicative success.

Author Contributions

E. Fedorenko developed the study concept, and E. Fedorenko, J. Gallee and Z. Balewski developed the study design. Testing and data collection were performed by E. Fedorenko, J. Gallee and Z. Balewski. Data analysis and interpretation was conducted by M. Kline and Z. Balewski under the supervision of E. Fedorenko. M. Kline drafted the manuscript, and E. Fedorenko provided critical revisions. All authors approved the final version of the manuscript for submission.

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Supplemental materials

A. Localizer quality evaluation: response of localized regions to (GCSS analysis)

All fROIs showed significant responses to their respective contrast, with the sole exception of the VMPFC ToM fROI, which was consequently excluded from the critical analyses. We report uncorrected significance values throughout, but all critical effects remain significant after an FDR correction for the number of fROIs in each system, with a few exceptions in the MD system (see tables below).

All language fROIs responded robustly to the Sentences>Nonwords contrast in both left-hemisphere (ts>4.78, ps<0.001), and right-hemisphere regions (ts>2.39 , ps<0.018, with the exception of the RAngG fROI, where the effect was marginal: t=1.79, p=0.051). The two conditions were also significantly different from one another by a linear mixed effects model with condition (sentences vs. nonwords) as a fixed effect and participant and fROI as random effects (LH: χ^2=14.87, p<0.001; RH: χ^2=8.91, p<0.001)[2].

Because participants performed only one run of the MD localizer task, the cross-validation of the localizer contrast across runs could not be performed. Instead, we examined the responses in the MD fROIs to the Nonwords>Sentences contrast, which has been previously shown to produce responses in these regions (Fedorenko et al., 2012, 2013). Indeed, this contrast was reliable in the MD fROIs in both left and right hemisphere (ts>1.87, ps<0.044), with the exception of the RSMA and LSMA fROIs, which showed marginal effects (t=1.58, p=0.07; and t=1.70, p=0.06, respectively), and the LPrecG fROI, which showed a trend (t=0.80, p=0.22). By a linear mixed effects model, the two conditions were significantly different from one another in both hemispheres (LH: χ^2=11.80, p<0.001; RH: χ^2=9.33, p=0.002). Given that a) the

[2] In all cases, LME models are fit using the lme4 package (Bates, Mächler, Bolker, & Walker, 2015) with maximal random effects structure and evaluated by comparison with a model with the same random effects structure and lacking the critical factor of interest, e.g.

```
m1 <-lmer(sigChange ~ contName + (contName|ROIName) + (contName|Subj)
m0 <-lmer(sigChange ~ 1 + (contName|ROIName) + (contName|Subj))
anova(m1,m0)
```

individual activation maps for the Hard>Easy contrast of the MD localizer task were robust, in with prior work (e.g., Fedorenko et al., 2013), and b) all fROIs showed at least a strong trend for the Nonwords>Sentences effect, we did not exclude any fROIs from the critical analyses.

Finally, the ToM fROIs[3] responded reliably to the False belief>False photograph contrast (ts>2.02, ps<0.039, except for the VMPFC, t=0.62, p>0.25; by linear mixed model χ^2=8.07, p<0.001). Because the VMPFC fROI did not show a reliable response to our Theory of Mind localizer contrast, we excluded it from the critical analyses.

[3] To allow for cross-validation, we included only participants (n=9) who completed two runs.

B. A traditional whole brain random effects analysis of the critical task

To complement the fROI-based analyses described above, we conducted a standard group-based analysis, where a t-test is performed in each voxel across participants for each relevant contrast (Friston, 2007). The table below shows the sizes, locations, and the uncorrected p-values for each of the nineteen clusters that emerged for the critical, Jokes>Non-jokes, contrast.

		Location of peak activation		
Cluster size (voxels)	p (uncorrected)	x	y	z
132	<0.001	-10	14	0
		-10	12	8
23	0.005	-28	-10	-14
49	<0.001	-44	-58	12
		-46	-60	20
		-52	-56	24
50	<0.001	-52	-8	-20
		-58	-12	-24
83	<0.001	-10	54	20
		-10	56	8
		-4	60	0
10	0.046	-16	-22	6
105	<0.001	-58	-50	42
		-54	-46	50
		-54	-38	46
13	0.026	0	-20	4
69	<0.001	-48	-68	40
		-44	-66	32

142	<0.001	-34	14	4
		-34	0	4
		-30	12	14
42	<0.001	8	16	-2
15	0.018	-52	4	32
		-48	4	24
53	<0.001	-40	32	26
		-46	34	34
32	0.001	60	-44	26
25	0.003	-32	-70	54
		-40	64	54
21	0.006	-50	-40	54
24	0.004	10	58	8
		12	54	-2
10	0.046	-30	-26	62
14	0.021	-56	-42	32

C. Tables of individual fROI t-tests for the responses to the localizer contrasts and to the critical contrast

In all tables uncorrected p values are reported; all tests marked with an asterisk (*) are significant after family-wise correction (by number of fROIs/system) for multiple comparisons.

Language fROIs (right and left hemisphere) responding to the language localizer contrast (Sentences > Nonwords, see Design & materials.)

fROI	t	p
RIFGorb	4.64	<0.001*
RIFG	5.066	<0.001*
RMFG	2.389	0.018*
RAntTemp	7.846	<0.001*
RPostTemp	5.338	<0.001*
RAngG	1.789	0.051

fROI	t	p
LIFGorb	8.554	<0.001*
LIFG	6.317	<0.001*
LMFG	6.085	<0.001*
LAntTemp	11.229	<0.001*
LPostTemp	9.48	<0.001*
LAngG	4.776	<0.001*

Multiple Demand fROIs (right and left hemisphere) responding to the Nonwords > Sentences contrast

fROI	t	p
RIFGop	2.32	0.020*
RMFG	3.915	0.001*
RMFGorb	4.121	<0.001*
RPrecG	1.871	0.044*
RInsula	2.141	0.028*
RSMA	1.578	0.071
RParInf	2.366	0.019*
RParSup	3.565	0.002*
RACC	3.809	0.001*

fROI	t	p
LIFGop	2.547	0.014*
LMFG	6.499	<0.001*
LMFGorb	4.593	<0.001*
LPrecG	0.801	0.220
LInsula	2.31	0.021*
LSMA	1.704	0.058
LParInf	5.455	<0.001*
LParSup	4.085	<0.001*
LACC	4.559	<0.001*

Theory of Mind fROIs responding to the False belief > False photo contrast

fROI	t	p
DMPFC	2.021	0.039*
LTPJ	8.672	<0.001*
MMPFC	2.116	0.034*
PC	4.287	0.001*
RTPJ	5.027	<0.001*
VMPFC	0.625	>0.025
RSTS	4.647	<0.001*

Language fROIs (right and left hemispheres) responding to the Jokes > Nonjokes contrast

fROI	t	p
RIFGorb	0.954	0.180
RIFG	0.462	>0.025
RMFG	0.828	0.213
RAntTemp	0.889	0.197
RPostTemp	1.692	0.059
RAngG	-0.237	>0.025

fROI	t	p
LIFGorb	1.619	0.067
LIFG	0.062	>0.025
LMFG	-0.799	>0.025
LAntTemp	1.75	0.054
LPostTemp	0.603	>0.025
LAngG	3.266	0.004*

Multiple Demand fROIs (right and left hemisphere) responding to the Jokes > Nonjokes contrast

fROI	t	p
RIFGop	-0.692	>0.025
RMFG	0.623	>0.025
RMFGorb	-0.523	>0.025
RPrecG	0.578	>0.025
RInsula	-0.375	>0.025
RSMA	1.081	0.151
RParInf	2.563	0.013
RParSup	0.837	0.210
RACC	1.284	0.113

fROI	t	p
LIFGop	2.043	0.033
LMFG	1.51	0.080
LMFGorb	0.871	0.201
LPrecG	3.708	0.002*
LInsula	2.431	0.017*
LSMA	1.44	0.089
LParInf	3.051	0.006*
LParSup	3.039	0.006*
LACC	1.757	0.053

Theory of Mind fROIs responding to the Jokes > Nonjokes contrast

fROI	t	p
DMPFC	1.779	0.051
LTPJ	3.358	0.003*
MMPFC	3.95	0.001*
PC	2.75	0.009*
RTPJ	2.723	0.010*
RSTS	1.245	0.120

Theory of Mind fROIs responding to task with individual ratings (parameterized contrast weighting high = 1, med = 0, low = -1)

fROI	t	p
DMPFC	1.3177	0.107
LTPJ	6.901	<0.001*
MMPFC	2.9343	0.007*
PC	4.952	<0.001*
RTPJ	3.0207	0.006*
RSTS	2.8364	0.008*

D. Materials for the critical Joke Comprehension task

Below are listed the 78 items (Joke and Non-joke versions) used in the critical humor-rating task (originally developed by Coulson & Williams 2005). In each pair, the critical words are matched for cloze probability (the likelihood that a naïve participant will supply a given word after reading the sentence up to that point), ensuring that any differences are not related to lower-level sentence processing difficulties.

- A committee keeps minutes and takes (hours/votes)
- A device for finding furniture in the dark is a (shin/candle)
- A good way to blow your mind is to smoke (gunpowder/heroin)
- A man who has lost ninety percent of his brain is called a (widower/zombie)
- A problem drinker is one who never (buys/quits)
- A replacement player hit a home run with my (girl/ball)
- A thoughtful wife has pork chops ready when her husband comes home from (fishing/working)
- A vacation is the shortest distance between two (paychecks/locations)
- All roads lead to Rome, and all detours lead to (profanity/somewhere)
- Another thing a small boy is constantly outgrowing is his (allowance/underwear)
- Another thing that has developed by leaps and bounds is modern (dance/science)
- Arguments between couples are healthy; sometimes they even prevent (marriage/breakups)
- Autobiography is an unrivaled vehicle for telling the truth about (others/somebody)
- By the time Mary had her fourteenth child, she'd run out of names to call her (husband/offspring)
- Charged with statutory rape, he told the judge he didn't know she was a (statue/teenager)
- Cocktails lounges are usually half lit to match the (patrons/setting)
- Congress taxes our income, our property, and our (patience/purchases)
- Diamonds are produced by great pressure, usually provided by a (girlfriend/piston)
- Every time I wear my spring coat in the rain, it damages the (springs/fabric)

- Everyone had so much fun diving from the tree into the swimming pool we decided to put in a little (water/platform)
- Figures don't lie, except on the (beaches/page)
- For great vacation, put the kids in the back seat, and take a (cruise/freeway)
- Frequent naps prevent old age, especially when taken while (driving/relaxed)
- He asked if I'd join him in a bowl of soup, but I told him we didn't have enough (room/change)
- He got a medal for bravery on the beach when he rescued a girl from a (lifeguard/shipwreck)
- He is at the age when all the numbers in his little black book belong to (doctors/friends)
- He is probably the best boxer in the country, but he always loses in the (city/competition)
- He likes to make things around the house; this week it's the (maid/shelves)
- He owns stock in a company that pays quarterly dividends, so every three months they send him a (quarter/statement)
- He says he doesn't like to drink because it makes him feel (happy/sad)
- He told her he wasn't himself, and she said she'd noticed the (improvement/problem)
- He told me he just bought a set of balloon tires, and I told him I didn't even know he owned a (balloon/truck)
- He told me he's not broke, just badly (bent/off)
- He was teaching his girlfriend how to swim when the lifeguard made them move to the ((lake/shallows))
- He's never given a girl a present, but he did give a few a pretty good (reputation/surprise)
- He's planning an extended vacation; he hopes to spend three weeks on his (couch/sailboat)
- Her press agent was operated on for an ingrown (beeper/eyelash)
- His doctor recommended he stay flat on his back ever since he was hit by a (steamroller/motorist)
- His wife sued for divorce and asked for custody of the (cash/cat)
- I asked him if he started out as an editor, and he said that years ago he used to be a (boy/journalist)

- I asked the florist what I should give to my girlfriend, and he suggested his (address/tulips)
- I asked the woman at the party if she remembered me from last year, and she said she never forgets a (dress/name)
- I can walk on water, but I stagger on (alcohol/concrete)
- I decided to start saving for a rainy day, so I went to a savings and loan and deposited my (umbrella/pay)
- I got a car for my wife, and I thought it was a good (trade/choice)
- I hope this train stops at Grand Central because if it doesn't, there will be a (crash/delay)
- I knew a streetwalker who was so exclusive she had an unlisted telephone (booth/line)
- I know one couple who got divorced and had to leave the house to the (attorney/daughter)
- I still miss my ex-wife, but I am improving my (aim/ego)
- I went to a place that serves breakfast any time and ordered French toast in the (Renaissance/nighttime)
- I've got Parkinson's disease, and he's got, (mine/gout)
- If there's one thing that counts in business, its (bookkeepers/resources)
- If you're filthy rich, sending your kids to college is a wonderful, (cleaner/luxury)
- In some marriages the bride is given away by the (press/family)
- In the game of golf, nothing counts as much as your (opponent/drives)
- It's always nicer to give than to receive, especially when its your (opinion/parents)
- It's extraordinary what fine poker hand you get when you're playing (bridge/stud)
- It's hard to raise a family nowadays, especially in the (morning/country)
- It's not hard to meet expenses; they're (everywhere/affordable)
- Last Thanksgiving my wife spent all morning in the kitchen stuffing the (kids/bird)
- Love has its benefits, and they are usually called (alimony/memories)
- Many a freshman helps the college of his choice by becoming a (dropout/member)

- Many a man's idea of a vacation is to rest quietly in the shade of a (blonde/palm)
- Many things run in families, especially (noses/strength)
- Modern science is amazing: garbage is now being made into (movies/gasoline)
- Most of the people running for office are not politicians; they're (commuters/candidates)
- My brother-in-law enjoys fixing things around the house so much he spent an hour last night just fixing our (drinks/stove)
- My church welcomes all denominations but prefers (twenties/Mormons)
- My doctor has never violated his oath: the oath he took years ago to become a (millionaire/practitioner)
- My husband took the money we were saving to buy a new car and blew it all at the (laundry/tables)
- My mechanic couldn't fix my brakes, so he fixed my (horn/clutch)
- My wife did natural childbirth: no (makeup/anesthetic)
- Nature has three ways of thinning the herd: drought, famine, and (primaries/hunting)
- No patient should leave the hospital until he's strong enough to face the (cashier/outside)
- Nothing ages a woman faster than (identification/hardship)
- Nothing in the known universe travels faster than (gossip/radiation)
- Nothing you put in a banana split is as potentially fattening as the (spoon/syrup)
- Now that the Hollywood couple has ironed out the divorce settlement, they can finally go ahead with their (nuptials/careers)
- Once a week they hold a bingo game, and all the proceeds go to fight (gambling/disease)
- One good turn gets most of the (blanket/profit)
- One good way to invest in the country is to buy a (senator/business)
- One person who sure makes a long story short is my (editor/aunt)
- One thing that makes the world go round is (detours/greed)
- One way to keep pornography away from teenagers is to put it in a (textbook/cabinet)

- Our son brought home a note from school saying they need a written excuse for his (presence/tardiness)
- Parents support clubs for teenagers, especially when they lack other forms of (punishment/diversion)
- Politicians who are as American as apple pie still want their (slice/rewards)
- Save the whales; start a (collection/coalition)
- She always told girls not to look for a husband but just to date (bachelors/someone)
- She asked what state he was born in, and he said in the (nude/East)
- She is so modest, she pulls down the shade to change her, (mind/jacket)
- She puts something behind her ears to attract men; lately she's been using her (ankles/vanilla)
- She read so much about the bad effects of cigarettes she decided to give up the (reading/habit)
- She told him he looked like a million, and she meant every (century/syllable)
- She went on a fourteen day diet, but she only lost two (weeks/ounces)
- She's happy because she finally has a boyfriend who gets along with her (fianc_/father)
- Some babies are born to rule, while others are (male/weak)
- Some husbands are good providers, but only if you count (children/salary)
- Some people think courtship is the first in a series of steps leading to (divorce/romance)
- Some people's only culture is (bacteria/radio)
- Statistics indicate that Americans spend eighty million a year on games of chance, (mostly/weddings), blackjack
- Sunday is the day we bow our heads and (putt/rest)
- The art museum just acquired an early Rembrandt; it's done in (Crayola/charcoal)
- The best bargain I ever got was when I went to a family garage sale and bought a (grandma/toaster)
- The best gift for the man who has everything is (penicillin/neckties)
- The best way to keep the milk from turning sour is to keep it in the (cow/cold)
- The best way to remove coffee stains from a white blouse is with (scissors/detergent)

- The best way to stop an elephant from charging is to cut off its (credit/toes)
- The book that tells you where you can go on vacation is called a (checkbook/guidebook)
- The convict told his cellmate how he'd blown all the money he stole on wine, women, and (lawyers/crack)
- The cops claimed that the prisoner just decided to come clean, but most people think he was forced into the (bathtub/admission)
- The curse of heavy drinking is that afterwards you get a (huge/bar) (tab/headache)
- The difference between a dog and fox is about five (beers/degrees)
- The difference between a good speaker and a bad one is often a nice (nap/diction)
- The first two hundred story building opened in Chicago; it was a (library/hotel)
- The husband who catches his wife in the act is probably on the (trapeze/snoop)
- The last time a guy in a mask took all my money I was in (surgery/shock)
- The most prevalent form of legalized gambling is (elections/betting)
- The new tax forms are more realistic: where your wife signs, it says (accomplice/partner)
- The only crop that is grown in America and harvested abroad is the American (tourist/tobacco)
- The only fishing through the ice that some men ever do is for the (olive/trout)
- The only ones who want me for my body are (mosquitos/losers)
- The only person who sticks closer to you in adversity than a friend is a (creditor/spouse)
- The only place where you can find people who spend all their time minding their own business is the (cemetery/bank)
- The only thing money can't buy is (poverty/generosity)
- The only time my father ever raised a hand to his children was in ,self- (defense/discipline)
- The penalty for dishonesty is the disgrace of dying (rich/unloved)
- The perfect companion to a vegetarian dinner is a (steak/salad)
- The show had one act that was really offbeat: the (singer/clowns)

- The tourist bureau told the visitors there was plenty of hunting in this part of the country but very little (finding/sightseeing)
- The wind was so strong it blew out three (fuses/streetlights)
- The woman who has her husband eating out of her hand must save a lot of (dishwashing/heartbreak)
- They redecorated the bar with new (drunks/wood)
- This fall two things are turning yellow: trees and (investors/bushes)
- This house comes with lots of extras, mostly (termites/upgrades)
- This new computer works so quickly, it comes complete with (ulcers/games)
- Though most people think it's Rome, the world's most beloved capital is actually (dollars/Vienna)
- To clothe one soldier, it takes the wool from two sheep and the hides from three (taxpayers/animals)
- To get something done, a committee should consist of no more than three people, two of whom are (dead/workers)
- Too many girls believe that the chief foundation for true love is a large (stone/fortune)
- Two things are essential for success: wealth and (money/fame)
- We live in a lovely suburb; it's just two miles beyond our (income/town)
- When an irresistible force meets an immovable object, you get two very angry (women/entities)
- When I asked how long he should cook the noodles, I said at least ten (inches/seconds)
- When I asked the bartender for something cold and full of rum, he recommended his (wife/daiquiri)
- When I found out how much my wife spent on dresses last year, I dumped her and proposed to the (dressmaker/mistress)
- When it comes to keeping warm, nothing beats a thermal (brunette/parka)
- When John bought a bulldog, it was no time at all before he had that dog eating out of his (leg/fingers)
- When reviewing your notes for a test, the most important ones will be (illegible/capitalized)
- When the kid came into the store and asked for empty boxes, the owner gave him the (register/crate)

- When we got divorced, my wife and I split the house; she got the (inside/kitchen)
- When we watch a sexy movie, my wife leans over and breathes on my (glasses/collar)
- When you own an ice cream business, your favorite flavor is (aspirin/everything)
- Where I'm from, the two most common elements are hydrogen and (stupidity/nitrogen)
- Women don't dress to please men; if they did, they'd dress a lot (faster/scantier)
- You can keep your kids in hot water with (dishes/rules)