



Understanding Sarcasm's Neural Correlates Through a Novel fMRI Spanish Paradigm

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Abstract

There is growing interest in the neural network of pragmatic language and its potential overlap with the Theory of Mind (ToM) network. However, no Spanish-adapted fMRI tasks were used for studying sarcasm, the subtype of pragmatic language most related to ToM. Furthermore, stimuli used in prior studies often impose high cognitive demands, confounding its sarcasm brain representation with the executive network. We investigate the neural correlates of sarcasm in Spanish using a novel experimental paradigm designed to minimize cognitive load and enhance ecological validity. Eighteen healthy, right-handed participants underwent a 3T fMRI session with a sarcasm comprehension task. Brain activations analysed with SPM12 were calculated for sarcasm vs. literal contrast. Sarcasm activated the left temporo-parietal junction, Medial Prefrontal Cortex (BA 10), Left Inferior Frontal Gyrus (BA 45), Left Medial and Superior Temporal Gyrus (BA 21 & 22), and Left Temporal Pole (BA 38). Sarcasm comprehension involves an extensive fronto-temporal-parietal network, with prominent activation of ToM-related areas. These findings suggest an overlap between sarcasm and ToM networks, emphasizing the role of the medial prefrontal cortex in pragmatic language, the left inferior frontal gyrus in semantic integration, and the role of a left-lateralized frontotemporal network for sarcasm processing.

Keywords ToM · Language · Pragmatic · Non-literal · Network · Neuroimage

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Introduction

Sitting at the back of the classroom, a student yawns while staring at their cell phone. The teacher notices this gesture and interrupts the lecture by commenting publicly, “Nice to see you paying attention back there.” Understanding the meaning of this remark might seem natural—the teacher is pointing out the student’s neglect. Nonetheless, the process of grasping this meaning is complex, involving several underlying questions: Does the teacher really mean what they literally say? If not, what are they trying to communicate? Do they expect the student to infer the true meaning behind their words?

Pragmatic language is ubiquitous, an everyday manner of addressing social interactions (Rapp et al. 2012). It is used to convey a meaning different from a literal understanding of the words (Bendersky et al. 2021; Bohrn et al. 2012). Because of this property, context claims a singular significance in pragmatic language, especially when it comes in the form of sarcasm (Tsolakopoulos et al. 2023). Sarcasm is a specific form of pragmatic language in which a speaker

conveys the opposite of what is literally said, often with the intention to criticize (Filik et al. 2019; Gibbs 1986; Matsui et al. 2016; Rankin et al. 2009), mock (Filik et al. 2019), or to be humorous (Kreuz and Glucksberg 1989). In the classroom example, the teacher's words sarcastically criticize the student's lack of attention. At this point, it is important to mention that, while sarcasm is frequently conflated with irony, the two differ in intentionality: irony broadly denotes non-literal communication without inherent criticism, whereas sarcasm explicitly aims to mock or ridicule (Filik et al. 2019). This distinction is critical, as many studies on "irony" employ sarcastic stimuli.

To grasp the actual meaning of sarcastic utterances, one must be able to (1) recognize that the speaker does not believe what they literally say (Pexman and Glenwright 2007; Winner and Gardner 1993), (2) recognize that the speaker intends the listener not to believe the literal meaning of the words (Parola et al. 2016; Winner and Gardner 1993), that is, to capture his sarcastic intentions (Pexman and Glenwright 2007). Should the listener lack these capacities, they could mistakenly understand that the speaker is either mistaken or lying, respectively (Pexman and Glenwright 2007; Winner and Gardner 1993).

Thus, sarcasm comprehension relies on more than just linguistic processing—it involves the ability to infer another person's thoughts, intentions, and emotions (Bohrn et al. 2012; Channon et al. 2005; Winner and Gardner 1993). This ability, known as Theory of Mind (ToM) or mentalization (Frith and Frith 2006; Winner and Gardner 1993), is essential since literal interpretation alone is insufficient for understanding sarcastic remarks (Valles-Capetillo et al. 2022). Additionally, sarcasm is communicated through contextual or paralinguistic cues, helping the listeners infer the speaker's true meaning (Kreuz and Glucksberg 1989; Matsui et al. 2016; Nakamura et al. 2022; Rankin et al. 2009; Uchiyama et al. 2006; Woodland and Voyer 2011). Contextual cues arise from the incongruity between the literal meaning of a sentence and the context in which it is spoken (Kreuz and Glucksberg 1989; Matsui et al. 2016; Nakamura et al. 2022; Rankin et al. 2009), while paralinguistic cues, such as prosody and facial expressions, reinforce the speaker's sarcastic intent (Matsui et al. 2016; Nakamura et al. 2022; Rankin et al. 2009; Valles-Capetillo et al. 2022).

In recent years, scientific interest in the neural correlates of sarcasm, and pragmatic language in general, has grown. Consequently, numerous neuroimaging studies have sought to map the neural substrates underlying this function, primarily examining whether these correlates overlap with the ToM network. In this context, four quantitative meta-analyses have synthesized results from neuroimaging studies to explore neural differences in processing literal versus pragmatic language, collectively underscoring the role of ToM

in pragmatic language comprehension (Bohrn et al. 2012; Hauptman et al. 2023; Rapp et al. 2012; Reyes-Aguilar et al. 2018). Hauptman et al. (2023) found that pragmatic language comprehension is supported by the ToM network. The remaining three of these studies further distinguish between subtypes of pragmatic language, such as metaphors, idiomatic expressions, proverbs and sarcasm. They reported that the two brain regions most consistently associated with sarcasm are the mPFC and left IFG, which are key nodes of the ToM network (Abu-Akel and Shamay-Tsoory 2011; Arioli et al. 2021; Arioli and Canessa 2019; Frith and Frith 2006; Schurz et al. 2014).

Activation in the mPFC is consistently observed across nearly all neuroimaging studies on sarcasm (Eviatar and Just 2006; Rapp et al. 2010, 2013; Uchiyama et al. 2006; Wang et al. 2006a; Bosco et al. 2017; Filik et al. 2019; Nakamura et al. 2022; Spotorno et al. 2012; Varga et al. 2013). Moreover, lesion studies associate mPFC atrophy with deficits in sarcasm comprehension and ToM (Rankin et al. 2009; Shamay-Tsoory et al. 2005), and fMRI studies comparing patients that struggle with sarcasm comprehension with controls consistently show reduced mPFC engagement during irony/sarcasm processing in the first group (Rapp et al. 2013; Varga et al. 2013; Herold et al. 2018; Wang et al. 2006a; Williams et al. 2013). The mPFC is highly involved in inferring others' attitudes and intentions in the ToM literature (Abu-Akel and Shamay-Tsoory 2011; Frith and Frith 2006; Schurz et al. 2014). Uchiyama et al. (2006) proposed that mPFC decodes the speaker's attitude in sarcasm, showing a strong connection between sarcasm processing and ToM, even to a greater extent than other types of pragmatic language (Bohrn et al. 2012).

Regarding the left IFG, Bohrn et al. (2012), Rapp et al. (2012), and Hauptman et al. (2023) consistently reported its activation across studies on pragmatic language, with Reyes-Aguilar et al. (2018) highlighting its specific role in understanding irony. According to several neuroimaging studies, the left IFG is involved in both ToM and semantic processing (Bosco et al. 2017; Filik et al. 2019; Herold et al. 2018; Matsui et al. 2016; Nakamura et al. 2022; Obert et al. 2016; Rapp et al. 2010; Spotorno et al. 2012; Uchiyama et al. 2006; Wang et al. 2006a, b). Given its critical role in these dual processes, Rapp et al. (2012) proposed that the left IFG is involved in selecting and evaluating the meanings of statements. This idea is further supported by Jang et al. (2013), who found left IFG activation during the interpretation of highly implicit utterances, and by Bosco et al. (2017), who demonstrated its importance in detecting both ironic and deceitful statements. Additionally, Spotorno et al. (2012) found increased functional connectivity between the mPFC and left IFG during sarcastic compared to literal

sentences, suggesting ToM integration with language processing during sarcasm interpretation.

Several studies have found activations in the left or bilateral superior temporal sulcus/gyrus (STS/STG), another crucial area of the ToM network (Abu-Akel and Shamay-Tsoory 2011; Arioli et al. 2021; Frith and Frith 2006), during pragmatic language tasks (Akimoto et al. 2014; Eviatar and Just 2006; Herold et al. 2018; Obert et al. 2016; Shibata et al. 2007; Varga et al. 2013; Wang et al. 2006a, b). The STS is implicated in multiple functions, including semantic processing (Friederici 2011; Murphy et al. 2023), decoding visuospatial cues in social interactions (Arioli and Canessa 2019), and relaying emotional signals between the TPJ and limbic system (Abu-Akel and Shamay-Tsoory 2011). As Hein and Knight (2008) noted, the role of the STS may vary depending on its co-activation: it can support the ToM network when coactivated with the mPFC, or aid speech processing when coactivated with the IFG—both functions being essential for interpreting sarcasm.

Other key ToM regions were reported in the sarcasm literature, such as the temporoparietal junction (TPJ) (Abu-Akel and Shamay-Tsoory 2011; Arioli et al. 2021; Arioli and Canessa 2019; Frith and Frith 2006; Schurz et al. 2014). For instance, several studies have reported TPJ activation (primarily bilaterally) either during the contextual processing phase preceding sarcasm (Herold et al. 2018; Varga et al. 2013) or throughout the task in general (Bosco et al. 2017; Spotorno et al. 2012). This suggests that the TPJ's role in sarcasm comprehension may be linked to understanding communicative intentions and the social context where this type of language occurs (Herold et al. 2018), consistent with ToM-related functions and its involvement in other forms of pragmatic language (Arioli and Canessa 2019; Bambini et al. 2011).

Still, no study has yet explored the neural substrates of sarcasm in the Spanish language, although efforts have been made to study other types of pragmatic language processing in Spanish (Bendersky et al. 2021; Elizalde Acevedo et al. 2025). That is, research regarding this topic has largely focused on English-speaking contexts, limiting the generalizability of findings to other populations. Given that over 330 million people worldwide are native Spanish speakers, exploring sarcasm in this language provides a culturally and linguistically diverse perspective, thereby promoting a more inclusive and representative science. Moreover, this approach enables the investigation of potential differences in the expression and interpretation of sarcasm that might remain undetected in studies focused solely on English. Additionally, existing sarcasm paradigms often impose a high cognitive load on participants by requiring them to retain and integrate prior information, potentially compromising ecological validity, engage networks not directly

related to the intrinsic processing of sarcasm, such as the general Multiple Demand Network (Diachek et al. 2020).

The study of sarcasm processing has clinical implications. It seems to depend on frontotemporal regions, also known as the social brain (supporting ToM skills besides other social cognition domains) (Arioli and Canessa 2019), which are often classified as “non-eloquent areas” (Herbet and Duffau 2020). As a result, epilepsy surgery protocols may underestimate their function, assuming minimal risk to language if resected. However, damage to these networks can cause subtle but significant deficits in social communication, as already mentioned. By developing a task that maps the neural correlates of sarcasm in Spanish, this study provides a potential tool to identify and preserve key hubs of pragmatic processing during temporal or frontal lobe resections, thereby refining preoperative risk stratification and improving long-term outcomes.

This study aims to explore the neural substrates of sarcasm processing in the Spanish language using a novel fMRI task designed to minimize cognitive load and increase ecological validity. By integrating multimodal (visual-linguistic) stimuli, the task seeks to isolate sarcasm-specific neural correlates, while reducing interference from executive networks associated with task complexity. It is hypothesized that sarcasm comprehension in Spanish will engage a bilateral frontotemporal neural network partially overlapping with the ToM network, consistent with the previous cross-linguistic findings abovementioned.

Materials and Methods

Participants

Healthy native Spanish speakers were recruited for this study from Estudios en Neurociencias y Sistemas Complejos (ENyS- CONICET), located at ‘Hospital El Cruce.’ The sample comprised 18 participants (9 males, 10 females) with a mean age of 24.33 years ($SD = 5.37$, range = 18–36) and a mean of 16.4 years of education ($SD = 2.98$, range = 12–23) for the full cohort. Seventeen participants were right-handed. Participants with neurological, mental or language disorders, visual impairments, or any MRI exclusion criteria were excluded. All participants gave informed consent to take part in the study, which was evaluated by the Ethics Committee of the Hospital El Cruce, according to the declaration of Helsinki. Participants did not receive financial compensation for their participation in the study.

Table 1 Evaluation and task results

	Mean	SD
Word accentuation test	24.76	2.76
Edinburgh Handedness Inventory	58.83	48.23
Baseline condition accuracy	70%	25%
Literal condition accuracy	71%	23%
Sarcasm condition accuracy	72%	19%
Total task accuracy	71%	12%

No significant differences were found between conditions

Instruments

The Edinburgh Inventory, a ten-item questionnaire, was used to assess hand dominance (Oldfield, 1971), while WAT (Word Accentuation Test) in Spanish (Del Ser et al., 1997) was used to assess verbal IQ because it is as a brief, validated screening tool to confirm verbal competence in a high-functioning sample, avoiding ceiling effects of standard IQ tests and minimizing participant burden. (Table 1).

Stimuli

A novel Spanish sarcasm event-related paradigm was used during fMRI scanning in this study. The paradigm was created by our research group, as well as validated at a behavioural level (for this process, see <https://osf.io/ghrjc/>). Stimuli consisted of sixty vignettes, each composed of cartoon-like characters accompanied by a written utterance. The paradigm was specifically developed to investigate sarcasm processing while minimizing cognitive load and enhancing ecological validity. Noteworthy, while full ecological validity is unattainable in an fMRI setting, our paradigm represents a compromise: it improves upon prior designs by incorporating multimodal cues, yet maintains the experimental control needed to isolate sarcasm-related processes.

The task was structured as follows (Fig. 1). Sixty different vignettes were presented, each displayed for 4500 ms with an interstimulus interval of 500 ms. These timing parameters were selected based on the validation of the task at the behavioural level (Ocampo et al., under review), indicating that 4500 ms allowed sufficient multimodal

Table 2 Brain activations by contrasts

Peak Regions	Hemisphere	MNI coordinates			Z-value	k
		x	y	z		
<i>Sarcasm vs. literal</i>						
AG (BA 39)	L	−58	−54	8	4.76	2069
STG (BA 22)	L	−62	−40	20	4.48	
MTG (BA 21)	L	−64	−30	0	4.48	
SMG (BA 40)	L	−34	−30	18	2.77	35
amPFC (BA 10)	L	−8	58	30	3.19	21
IFG (BA 44, 45, 47)	L	−52	14	14	3.28	435
Insula (BA 13)	L	−38	−4	2	2.90	
Amygdala	L	−16	−6	−16	3.88	143
TP (BA 38)	L	−50	6	−24	3.33	108
VC (BA 17, 18, 19)	L	−10	68	−8	4.44	1071
VM (BA 7)	L	−8	−44	52	2.91	25
PreM (BA 6)	L	−46	−2	46	4.30	829
<i>Sarcasm vs. baseline</i>						
AG (BA 39)	L	−58	−58	10	3.27	224
MTG (BA 21)	L	−50	−24	−10	2.89	39
FEF (BA 8)	L	−14	34	50	3.81	133
dIPFC (BA 9)	L	−16	52	32	3.02	
Amygdala	L	−8	−4	−20	3.41	21
SMG (BA 40)	L	−46	−40	42	2.81	50
dPCC (BA 31)	L	−6	−54	34	2.58	36
VC (BA 18, 19)	L	−10	−64	−6	4.51	1018
PreM (BA 6)	L	−16	−16	68	3.60	85
PriM (BA 4)	B	−16	−28	74	3.38	74
PriS (BA 1)	L	−38	−20	36	2.76	110

Abbreviations: AG = angular gyrus; STG = superior temporal gyrus; MTG = medial temporal gyrus; SMG = supramarginal gyrus; amPFC = anterior medial prefrontal cortex; IFG = inferior frontal gyrus; TP = temporal pole; VC = visual cortex; VM = visuomotor cortex; PreM = premotor cortex; FEF = frontal eye fields; dIPFC = dorsolateral prefrontal cortex; dPCC = dorsal posterior cingulate cortex; PriM = primary motor cortex; PriS = primary somatosensory cortex; Hem = hemisphere; k = cluster size (number of voxels); BA = Brodmann area

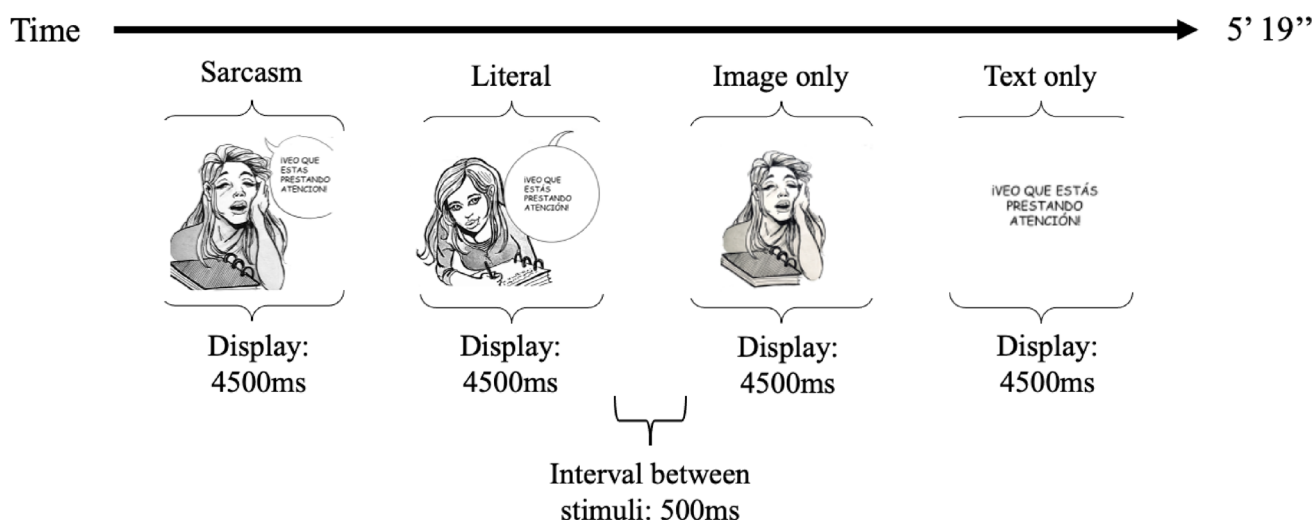


Fig. 1 Graphic representation of sarcasm paradigm. The figure shows four different types of stimuli used in the task (English: “I see you’re paying attention!”/Spanish: “¡Veo que estás prestando atención!”),

processing and natural response formulation while avoiding rushed decisions (shorter durations) or over-reflection (longer durations), preserving ecological validity. The vignettes were divided into three categories: (1) a sarcastic condition consisting of 20 vignettes, (2) a literal condition consisting of 20 vignettes, and (3) a baseline condition consisting of 20 vignettes, evenly including image-only and text-only stimuli. The total duration of the task was 5 min and 19 s. The design of the paradigm was event related.

The order of stimulus presentation was optimized using Chris Rorden’s fMRI Design Software. This tool generates sequences that maximize the statistical power of event-related designs by improving the efficiency of beta weight estimation for specific conditions or contrasts. The software accounts for experiment duration, TR (repetition time), stimulus duration, and frequency to minimize noise-related variance and enhance design efficiency. This optimization is critical in event-related paradigms to ensure robust detection of neural correlates (fMRI Simulator. <http://www.mccauslandcenter.sc.edu/CRNL/tools/fmrisim>). All participants were exposed to the same order of stimuli.

To ensure comparability between the sarcastic and literal conditions, each sarcastic vignette was paired with a literal counterpart. The written utterances were identical in both conditions (e.g., “¡Veo que estás prestando atención!”, which translates to “I see you’re paying attention!”). The distinction between sarcasm and literal meaning was conveyed through changes in the image context and the character’s expressions (e.g., the student was either paying attention or not). This design allowed for a direct contrast between the two language conditions, isolating the neural correlates specific to sarcasm processing. Similarly, text-only stimuli of the baseline condition presented the same

one for sarcasm, one for literal, and two for the baseline (only text and only image). The total time of the task can be observed, as well as the display time of the vignettes and the interval between them

written utterance but lacked context, while image-only stimuli lacked the written utterance.

Stimuli were presented with E-prime software (Psychology Software Tools, Pittsburgh, PA, USA). The task script, images, and stimulus presentation order are openly available on the Open Science Framework (see <https://osf.io/hb28f/>). During the task, participants were required to report the type of stimuli displayed via a right hand four keys response box. Accuracy and response time were measured during the task. Before entering the scanner, participants were trained on a small subset of vignettes to familiarize them with the task and ensure accurate performance. During task performance, all trials - including those with incorrect responses - were retained for analysis. This decision was based on binomial tests confirming all participants performed significantly above chance level (20%, $p < 0.05$), indicating meaningful task engagement.

Image Acquisition

Structural and functional MRI data for the entire brain were acquired using a 3 T Philips Achieva scanner with the following acquisition sequences. For structural images, a high-resolution 3D T1-weighted sequence (Cartesian Plane) was acquired in the sagittal plane with the following parameters: repetition time (TR) = 7.0 ms, echo time (TE) = 3.2 ms, flip angle (FA) = 10°, field of view (FOV) in-plane = 240 × 240 mm, matrix size = 240 × 240, phase encoding in both antero-posterior, 180 slices acquired in 3D mode, Nav = 1 (signal averaging), voxel size = 1 × 1 × 1 mm³, and acquisition bandwidth = 191.5 Hz/pixel. Images were reconstructed with an in-plane interpolation factor of 2. Additionally, a

field mapping sequence was obtained to correct geometric distortions due to magnetic field inhomogeneities.

Functional images were acquired using a T2-weighted BOLD-sensitive sequence. A single run consisting of 4 dummy scans and 102 volumes was collected, 35 slices per volume. Acquisition was performed following the AC–PC (anterior commissure–posterior commissure) orientation. Each slice had a resolution of 96×94 pixels with a voxel size of $2.4 \times 2.4 \times 3.5$ mm³, no inter-slice gap, a slice thickness of 3.5 mm, and slices were acquired in an interleaved manner. Volumes were recorded with TR = 1490 ms, TE = 35 ms, and FA = 90°. The total duration of the functional run was 5 min and 19 s.

Image Processing

Data were processed following the steps described in previous studies (Alba-Ferrara et al. 2016; Bendersky et al. 2021; Elizalde Acevedo et al. 2025; Olano et al. 2020). Image pre-processing and statistical analyses were performed using the SPM12 software package (Wellcome Department of Cognitive Neurology; <https://www.fil.ion.ucl.ac.uk/spm>). The functional images were subjected to geometric distortion correction and motion correction. A mean functional image was calculated from the unwarped and motion-corrected volumes. The structural (T1-weighted) images were co-registered to the mean functional image for each subject. Subsequently, the structural images were segmented into gray and white matter. The segmented gray matter images (both functional and structural) were normalized to Montreal Neurological Institute (MNI) space. The normalized images were resampled as needed and smoothed with an 8 mm full-width at half maximum (FWHM) Gaussian kernel. A 128 s high-pass filter was applied to remove low-frequency drifts. Additionally, estimated head motion parameters (from the realignment step) and other nuisance regressors (e.g., mean signals from whole brain, ventricles, and white matter) were included in the design matrix to reduce non-neuronal variability.

First-level statistical analysis was based on a general linear model (GLM) (Friston et al. 1995). The time series was high-pass filtered with a 128 s cut off and convolved with the canonical hemodynamic response function (HRF) to model the expected response. In addition, global scaling was applied per session. The design matrix included four regressors of interest corresponding to the task conditions: Sarcasm, Literal, Image Only, and Text Only. Events were modeled as a function of stimulus onset, with a fixed duration corresponding to stimulus presentation. The “Image Only” and “Text Only” regressors were pooled and used as the baseline condition. Individual contrast maps (first level) were calculated for each main condition. For the

second-level analyses (group), a one-sample t-test was performed to compare the Sarcasm > Literal and Sarcasm > Baseline conditions. The last contrast was performed to isolate sarcasm-specific neural activity by subtracting low-level sensory and task-related unspecific cognitive processing captured in the baseline condition. Parameter estimates were obtained using an ordinary least squares adjustment.

For each contrast, masking was performed using the Neuromorphometrics Atlas (<https://www.neuromorphometrics.com/>) to restrict analyses to gray matter regions, excluding white matter and ventricular cerebrospinal fluid. Finally, one-sample t-tests were conducted on the contrast images using SPM12. Statistical maps were thresholded at an uncorrected p-value of < 0.01. We chose to employ Monte-Carlo correction of the brain volume to establish an appropriate voxel contiguity threshold (Slotnick and Schacter 2004). This correction has the advantage of higher sensitivity to smaller effect sizes, while still correcting for multiple comparisons across the whole brain volume. The procedure is based on the fact that the probability of observing clusters of activity due to voxel-wise Type I error (i.e., noise) decreases systematically as cluster size increases. Therefore, the cluster extent threshold can be determined to ensure an acceptable level of corrected cluster-wise Type I error. Similar procedures have been used previously to estimate fMRI spatial correlation (e.g., see Katanoda et al. 2002; Ross and Slotnick 2008). An individual voxel threshold was then applied to achieve the assumed voxel-wise Type I error rate ($P < 0.01$). The probability of observing a given cluster extent was computed across iterations under $P < 0.05$ (corrected for multiple comparisons).

Results

Behavioural Performance

Recorded participants successfully performed the task. The instruments and task response results are presented in Table 1. A repeated measures ANOVA revealed no significant differences in accuracy across conditions.

Neuroimaging Results

Sarcasm Vs. Literal

The sarcasm vs. literal contrasts elicited left-lateralized activations along the Angular Gyrus (BA 39), Supramarginal Gyrus (BA 40), Superior Temporal Gyrus (BA 22), Medial Temporal Gyrus (BA 21), anteromedial Prefrontal Cortex (BA 10), Inferior Frontal Gyrus (BA 44, 45, 47), Amygdala, Temporal Pole (BA 38), Insula (BA 13), Visual Cortex (BA

17, 18, 19), Visuomotor Cortex (BA 7), and Premotor and Supplementary Motor Cortex (BA 6) (Table 1; Fig. 2).

Sarcasm Vs. Baseline

The sarcasm vs. baseline contrasts showed activations in the left Angular Gyrus (BA 39), left Supramarginal Gyrus (BA 40), left Medial Temporal Gyrus (BA 21), left Frontal Eye Field (BA 8), left Dorsolateral Prefrontal Cortex (BA 9), right Anterior Prefrontal Cortex (BA 10), left Amygdala, left Dorsolateral Posterior Cingulate Cortex (BA 31), left Secondary Visual Cortex (BA 18), left Visual Association Cortex (BA 19), bilateral Primary Motor Cortex (BA 4), left Premotor and Supplementary Motor Cortex (BA 6), and left Primary Sensory Cortex (BA 1) (Table 1; Fig. 3).

Discussion

This study aimed to explore the neural correlates of sarcasm in the Spanish language using a novel fMRI paradigm. While the small sample size limits generalizability, results suggest that brain areas typically associated with ToM are also involved in sarcasm processing. That is, in the sarcasm vs. literal contrast, four core ToM regions (mPFC, IFG,

TPJ, and STS) showed significant left lateralized activation, which may support the hypothesis of overlap between sarcasm and ToM networks, broadly consistent with prior studies (Bohrn et al. 2012; Bosco et al. 2017; Channon et al. 2005; Eviatar and Just 2006; Filik et al. 2019; Hauptman et al. 2023; Nakamura et al. 2022; Rankin et al. 2009; Rapp et al. 2010, 2012, 2013; Shamay-Tsoory et al. 2005; Spotorno et al. 2012; Uchiyama et al. 2006, 2012; Varga et al. 2013; Wang et al. 2006a).

However, activations were not restricted to ToM regions. Additional left-lateralized areas, including the amygdala, insula, temporal pole, the posterior medial temporal gyrus (pMTG) and the posterior inferior temporal gyrus (pITG), were also recruited. This broader activation pattern may reflect involvement of high-level semantic and contextual integration processes, rather than ToM mechanisms alone. Sarcasm processing may begin with the fusiform gyrus, a key region in detecting visual language information (Elizalde Acevedo et al., 2025). Concurrently, emotionally salient cues could be processed by the amygdala (Matsui et al. 2016; Nakamura et al. 2022; Rankin et al. 2009; Uchiyama et al. 2012). These inputs might trigger parallel streams which overlap in several areas: one dedicated to linguistic decoding and another to ToM-based inference.

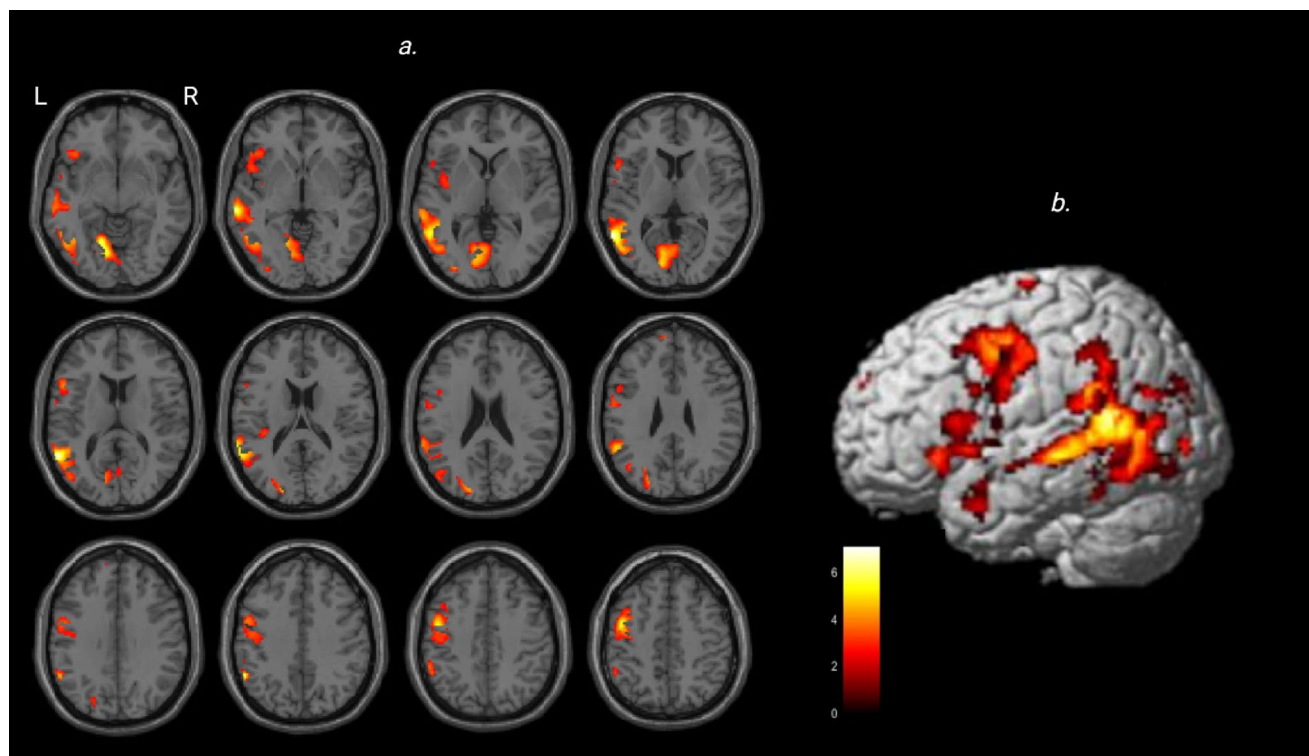


Fig. 2 Overview of sarcasm vs. literal contrast activations. Panel (a) depicts axial slices, and panel (b) illustrates a sagittal template of the same contrast. The sagittal view in (b) explicitly highlights the left-hemispheric distribution of activations. A primary cluster spans the

angular and supramarginal gyri, extending anteriorly to the superior and medial temporal gyri and encompassing the temporoparietal junction. A second cluster is visible along the three cytoarchitectonic subdivisions of the inferior frontal gyrus

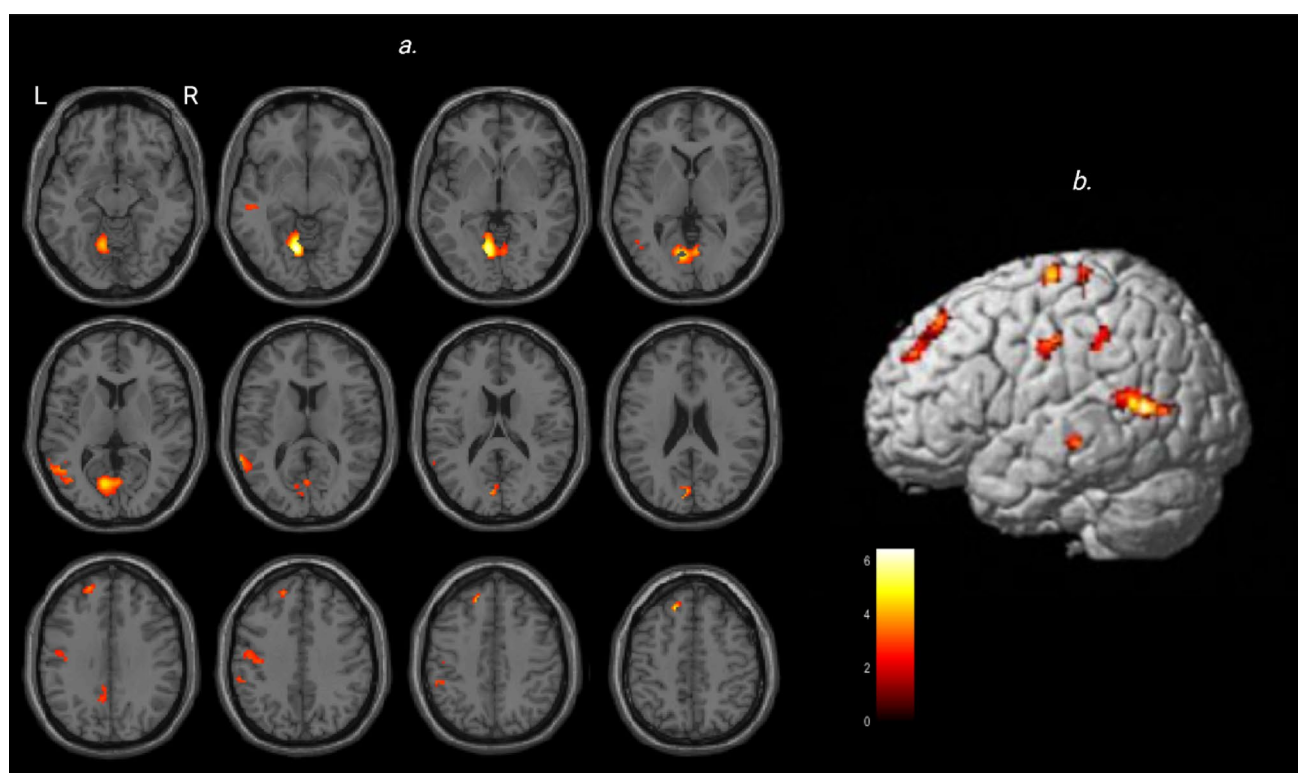


Fig. 3 Overview of sarcasm vs. baseline contrast activations. Panel (a) shows axial slices, while panel (b) displays a sagittal template of the same contrast. The sagittal view in (b) highlights the involvement of the left hemisphere, consistent with the overall left-lateralization

observed in the results. The main cluster extends across the frontal fields and dorsolateral prefrontal cortex. Significant activations are also observed in the angular and supramarginal gyri

Linguistic Processing Pathway

Semantic and syntactic information may initially be processed by the left pSTS (Friederici 2011; Murphy et al. 2023), supported by the left pMTG for semantic decoding (Murphy et al. 2023). These areas could prepare initial representations of phrases, which are then refined by the posterior IFG (BA 44/45), enabling the formation and evaluation of coherent linguistic structures (Friederici 2011). Notably, stronger activations in the sarcasm condition raise the possibility of higher linguistic complexity in pragmatic language compared to literal, or may reflect interconnections with other networks, such as the ToM network (Hauptman et al. 2023). As our paradigm controlled for syntactic complexity across conditions—phrases were the same, with context being the variable—this could be interpreted as tentative support for a higher network integration during sarcasm comprehension. However, the linguistic complexity of sarcasm may also stem from its inherent ambiguity; as mentioned before, both mistaken and deceitful utterances may be possible alternatives when a sarcasm phrase is presented (Pexman and Glenwright 2007; Winner and Gardner 1993). Semantic ambiguities have been shown to engage the left posterior temporal cortex, including the pSTS, pMTG, and

pITG, as part of a broader temporo-frontal network that also includes the left IFG (Friederici 2011).

In this regard, the left pMTG may play a crucial role during sarcasm comprehension. Bosco et al. (2017) reported that the MTG was more active for sarcastic sentences than for literal or deceptive ones, hypothesizing that the left MTG may aid in distinguishing utterances based on shared contextual knowledge between speakers. In addition, recent findings have positioned the left pMTG as a critical node in resolving semantic narrowing, defined as the process by which the range of possible meanings is incrementally reduced based on semantic and contextual cues (Murphy et al. 2023). In the context of sarcasm, semantic narrowing may help reduce interpretative ambiguity when contextual cues are strong. If contextual cues clearly indicate sarcasm, the left pMTG may efficiently limit the interpretative space, guiding rapid inferences. However, sarcasm also involves reconciling ambiguities or contradictions between literal and intended meanings. Thus, this dual demand may help to explain extended activations in the left pMTG. This interpretation would complement Bosco et al. (2017) view, plus it may underscore the dynamic interplay between semantic and other networks, such as the ToM, in this complex linguistic process (Hauptman et al. 2023).

ToM and Contextual Processing Pathway

Simultaneously, ToM processes may infer the speaker's intentions and contextual nuances during sarcasm comprehension. The TPJ is central to representing others' mental states (Abu-Akel and Shamay-Tsoory 2011; Arioli and Canessa 2019), while the mPFC infers attitudes/intentions (Uchiyama et al. 2006) and detects incongruencies between the literal meaning and contextual reality (Arioli and Canessa 2019; Nakamura et al. 2022). The left insula, closely interacting with the amygdala, also contributes through empathy-related processing (Arioli et al. 2021) and appraising emotional cues (Phan et al. 2002). Specifically, the left insula and amygdala likely assess the emotional salience of external stimuli, thus detecting emotional cues used by the ToM network for decoding intentions during sarcasm comprehension (Matsui et al. 2016; Nakamura et al. 2022; Rankin et al. 2009; Uchiyama et al. 2012).

Notably, the TPJ has also been shown to play a role in contextual processing prior to sarcasm detection (Herold et al. 2018; Varga et al. 2013), particularly in paradigms requiring extensive contextual preparation before sarcastic expressions (Bosco et al. 2017; Spotorno et al. 2012). Additionally, different parts of the TPJ have been linked to linguistic processes, such as the left STS and the left AG. The pSTS, as mentioned, has been identified as a key syntactic and semantic processing area (Friederici 2011; Murphy et al. 2023). Hein and Knight (2008) proposed that the function of this area may vary depending on whether it coactivates with the mPFC or the IFG. Based on this proposal, it could be argued that the left STS, prominent in the sarcasm vs. literal contrast, has a dual role in sarcasm comprehension: (1) in conjunction with the left IFG, it contributes to the high-level semantic processing required for understanding sarcasm; and (2) it supports ToM processes in the mPFC (also see Akimoto et al. 2014). On the other hand, AG has also been linked to contextual integration during narrative comprehension (Branzi et al. 2021), and in both semantic and non-semantic tasks (Branzi and Lambon Ralph 2023). It may act as a buffer for contextual and semantic information, aiding in the online processing of linguistically demanding tasks (Branzi and Lambon Ralph 2023).

Taken together, this evidence suggests the multifaceted role of the TPJ in sarcasm processing. In addition to its discussed role in representing mental states, the TPJ also appears to contribute to linguistic, non-ToM related processes, particularly through buffering and integrating contextual and semantic information. The dual role of these areas could be further supported by the recent meta-analysis conducted by Hauptman et al. (2023), which demonstrated that comprehension of non-literal language recruited both ToM and linguistic networks. Consequently, this tentatively

supports the view that sarcasm processing relies on an integrated interplay between ToM and linguistic networks (Hauptman et al. 2023; Paunov 2018).

Integration and Resolution Through a ToM and Semantic Related Area

Both streams might converge in the pars triangularis and pars orbitalis of the IFG (BA 45/47), regions implicated in context integration during both semantic and non-semantic tasks (Branzi and Lambon Ralph 2023), and to ToM processes (Abu-Akel and Shamay-Tsoory 2011; Arioli et al. 2021; Schurz et al. 2014). The IFG has already been associated with an integrative function in sarcasm comprehension (Matsui et al. 2016; Nakamura et al. 2022), as a region involved in dual semantic and ToM processes (Bosco et al. 2017; Filik et al. 2019; Herold et al. 2018; Obert et al. 2016; Rapp et al. 2010; Spotorno et al. 2012; Uchiyama et al. 2006; Wang et al. 2006a, b), and as a convergence point of semantic and emotional processes (Belyk et al. 2017). Additionally, it has been identified as a multi-domain area involved in detecting incongruencies and prediction violations across various cognitive tasks (Branzi and Lambon Ralph 2023). In the case of sarcasm, this integrative function would not act in isolation; rather, it likely operates in conjunction with the mPFC, which, as previously discussed, aids in detecting the inherent context-content incongruence characteristic of sarcastic expressions (Nakamura et al. 2022); both areas also coactivate more strongly during sarcasm processing than the literal one (Spotorno et al. 2012).

Furthermore, this hypothesis aligns with a frontotemporal progression of semantic processing (Murphy et al. 2023). The IFG may evaluate the possible meanings of an utterance by determining whether it is semantically coherent and contextually congruent (Friederici et al., 2011; Murphy et al. 2023). Given its integrative and violation prediction role, it could possibly assess whether plausible meanings align with the speaker's inferred mental state and intentions. That is, given its privileged position within the network, the IFG may serve as the final integration site where the sarcastic meaning is evaluated, selected and consolidated (Bosco et al. 2017; Rapp et al. 2012).

Conclusion

This study offers preliminary insights regarding the neural correlates of sarcasm comprehension in Spanish, revealing that sarcasm processing may recruit an extensive left-lateralized fronto-temporal-parietal network. Notably, our findings point to a potential overlap between sarcasm and ToM networks, in general alignment with prior research.

However, sarcasm comprehension also appears to engage additional regions beyond those traditionally associated with ToM, highlighting the involvement of high-level linguistic processes, such as semantic integration, contextual decoding, and ambiguity resolution.

The overlap between sarcasm and ToM-related regions, including the mPFC, TPJ, STS, and IFG, may also reflect the complex linguistic demands required for sarcasm comprehension. For instance, the left pMTG may play a critical role in resolving semantic narrowing and integrating contextual cues, while the anterior portions of IFG could serve as a convergence point for two parallel pathways related to semantic and ToM processes. These regions could support mentalizing functions and the dynamic interplay between linguistic and contextual inference.

Our findings should be interpreted with caution due to the modest sample size, but they contribute to the ongoing discussion of how ToM and language networks interact during the comprehension of pragmatic language. Given the heavy reliance of sarcasm on ToM, studying this form of language provides a unique lens to explore the intricate relationship between these networks. By deepening our understanding of the neural architecture supporting sarcasm comprehension through a novel ecological Spanish task, this study highlights the potential value of investigating pragmatic language as a means to bridge the gap between linguistic and social neurological processes.

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Data Availability Materials and data for the study are available at <https://osf.io/ghrjc/> and <https://osf.io/hb28f/>.

Declarations

Competing Interests The authors declare no competing interests.

Consent To Participate Informed consent was obtained from all individual participants included in this study.

Open Practices The study in this article earned an Open Data — Protected Access badge for transparent practices. Materials and data for the study are available at <https://osf.io/hb28f/>.

References

- Abu-Akel A, Shamay-Tsoory S (2011) Neuroanatomical and neurochemical bases of theory of Mind. *Neuropsychologia* 49(11):2971–2984. <https://doi.org/10.1016/j.neuropsychologia.2011.07.012>
- Akimoto Y, Sugiura M, Yomogida Y, Miyauchi CM, Miyazawa S, Kawashima R (2014) Irony comprehension: social conceptual knowledge and emotional response. *Hum Brain Mapp* 35(4):1167–1178. <https://doi.org/10.1002/hbm.22242>
- Alba-Ferrara L, Müller-Oehring EM, Sullivan EV, Pfefferbaum A, Schulte T (2016) Brain responses to emotional salience and reward in alcohol use disorder. *Brain Imaging Behav* 10:136–146. <https://doi.org/10.1016/j.neuropsychologia.2020.107580>
- Arioli M, Canessa N (2019) Neural processing of social interaction: Coordinate-based meta-analytic evidence from human neuroimaging studies. *Hum Brain Mapp* 40(13):3712–3737. <https://doi.org/10.1002/hbm.24627>
- Arioli M, Cattaneo Z, Ricciardi E, Canessa N (2021) Overlapping and specific neural correlates for empathizing, affective mentalizing, and cognitive mentalizing: A coordinate-based meta-analytic study. *Hum Brain Mapp* 42(14):4777–4804. <https://doi.org/10.1002/hbm.25570>
- Bambini V, Gentili C, Ricciardi E, Bertinetto PM, Pietrini P (2011) Decomposing metaphor processing at the cognitive and neural level through functional magnetic resonance imaging. *Brain Res Bull* 86(3–4):203–216. <https://doi.org/10.1016/j.brainresbull.2011.07.015>
- Belyk M, Brown S, Lim J, Kotz SA (2017) Convergence of semantics and emotional expression within the IFG pars orbitalis. *NeuroImage*, 156(2017), 240–248. <https://doi.org/10.1016/j.neuroimage.2017.04.020>
- Bendersky M, Lomlomdjian C, Abusamra V, Elizalde Acevedo B, Kochen S, Alba-Ferrara L (2021) Functional anatomy of idiomatic expressions. *Brain Topogr* 34(4):489–503. <https://doi.org/10.1007/s10548-021-00843-3>
- Bohrn IC, Altmann U, Jacobs AM (2012) Looking at the brains behind figurative language-A quantitative meta-analysis of neuroimaging studies on metaphor, idiom, and irony processing. *Neuropsychologia* 50(11):2669–2683. <https://doi.org/10.1016/j.neuropsychologia.2012.07.021>
- Bosco FM, Parola A, Valentini MC, Morese R (2017) Neural correlates underlying the comprehension of deceitful and ironic communicative intentions. *Cortex* 94:73–86. <https://doi.org/10.1016/j.cortex.2017.06.010>
- Branzi FM, Lambon Ralph MA (2023) Semantic-specific and domain-general mechanisms for integration and update of contextual information. *Hum Brain Mapp* 44(17):5547–5566. <https://doi.org/10.1002/hbm.26454>
- Branzi FM, Pobric G, Jung J, Lambon Ralph MA (2021) The left angular gyrus is causally involved in Context-dependent integration and associative encoding during narrative reading. *J Cogn Neurosci* 33(6):1082–1095. https://doi.org/10.1162/jocn_a_01698
- Channon S, Pellijeff A, Rule A (2005) Social cognition after head injury: sarcasm and theory of Mind. *Brain Lang* 93(2):123–134. <https://doi.org/10.1016/j.bandl.2004.09.002>
- Del Ser T, González-Montalvo JI, Martínez-Espinosa S, Delgado-Villalpalos C, Bermejo F (1997) Estimation of premorbid intelligence in spanish people with the word accentuation test and its application to the diagnosis of dementia. *Brain Cogn* 33(3):343–356. <https://doi.org/10.1006/brcg.1997.0877>
- 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. *J Neurosci* 40(23):4536–4550. <https://doi.org/10.1523/JNEUROSCI.2036-19.2020>
- Elizalde Acevedo B, Kochen S, Alba-Ferrara L, Bendersky M (2025) Reorganization of pragmatic Language networks in patients with Temporal lobe epilepsy. *Clin Neurophysiol* 147. <https://doi.org/10.1016/j.clinph.2024.12.012>
- Eviatar Z, Just MA (2006) Brain correlates of discourse processing: an fMRI investigation of irony and conventional metaphor comprehension Zohar eviatar and Marcel Adam just. *Processing* 44(12):2348–2359. <https://www.ncbi.nlm.nih.gov/pmc/articles/PMC1894906/pdf/nihms12946.pdf>
- Filik R, Turcan A, Ralph-Nearman C, Pitiot A (2019) What is the difference between irony and sarcasm? An fMRI study. *Cortex* 115:112–122. <https://doi.org/10.1016/j.cortex.2019.01.025>
- Friederici AD (2011) The brain basis of Language processing: from structure to function. *Physiol Rev* 91(4):1357–1392. <https://doi.org/10.1152/physrev.00006.2011>
- Friston KJ, Holmes AP, Poline JB, Grasby PJ, Williams SC, Frackowiak RS, Turner R (1995) Analysis of fMRI time-series revisited. *NeuroImage* 2(1):45–53. <https://doi.org/10.1006/nimg.1995.1007>
- Frith CD, Frith U (2006) The neural basis of mentalizing. *Neuron* 50(4):531–534. <https://doi.org/10.1016/j.neuron.2006.05.001>
- Gibbs RW (1986) On the psycholinguistics of sarcasm. *J Exp Psychol Gen* 115(1):3–15. <https://doi.org/10.1037/0096-3445.115.1.3>
- Hauptman M, Blank I, Fedorenko E (2023) Non-literal Language processing is jointly supported by the Language and theory of Mind networks: evidence from a novel meta-analytic fMRI approach. *Cortex* 162:96–114. <https://doi.org/10.1016/j.cortex.2023.01.013>
- Hein G, Knight RT (2008) Superior Temporal Sulcus—It's my area: or is it? *J Cogn Neurosci* 20(12):2125–2136. <https://doi.org/10.1162/jocn.2008.20148>
- Herbet G, Duffau H (2020) Revisiting the functional anatomy of the human brain: toward a meta-networking theory of cerebral functions. *Physiol Rev* 100(3):1181–1228. <https://doi.org/10.1152/physrev.00033.2019>
- Herold R, Varga E, Hajnal A, Hamvas E, Berecz H, Tóth B, Tényi T (2018) Altered neural activity during irony comprehension in unaffected First-Degree relatives of schizophrenia Patients—An fMRI study. *Front Psychol* 8(JAN):1–15. <https://doi.org/10.3389/fpsyg.2017.02309>
- Jang G, Yoon SA, Lee SE, Park H, Kim J, Ko JH, Park HJ (2013) Everyday conversation requires cognitive inference: neural bases of comprehending implicated meanings in conversations. *NeuroImage* 81:61–72. <https://doi.org/10.1016/j.neuroimage.2013.05.027>
- Katanoda K, Matsuda Y, Sugishita M (2002) A spatio-temporal regression model for the analysis of functional MRI data. *NeuroImage* 17(3):1415–1428. <https://doi.org/10.1006/nimg.2002.1209>
- Kreuz RJ, Glucksberg S (1989) How to be sarcastic: the echoic reminder theory of verbal irony. *J Exp Psychol Gen* 118(4):374–386. <https://doi.org/10.1037/0096-3445.118.4.374>
- Matsui T, Nakamura T, Utsumi A, Sasaki AT, Koike T, Yoshida Y, Harada T, Tanabe HC, Sadato N (2016) The role of prosody and context in sarcasm comprehension: behavioral and fMRI evidence. *Neuropsychologia* 87:74–84. <https://doi.org/10.1016/j.neuropsychologia.2016.04.031>
- Murphy E, Forseth KJ, Donos C, Snyder KM, Rollo PS, Tandon N (2023) The Spatiotemporal dynamics of semantic integration in the human brain. *Nat Commun* 14(1):6336. <https://doi.org/10.1038/s41467-023-42087-8>
- Nakamura T, Matsui T, Utsumi A, Sumiya M, Nakagawa E, Sadato N (2022) Context-prosody interaction in sarcasm comprehension: A functional magnetic resonance imaging study. *Neuropsychologia* 170(March):108213. <https://doi.org/10.1016/j.neuropsychologia.2022.108213>
- Obert A, Gierski F, Calmus A, Flucher A, Portefaix C, Pierot L, Kaladjian A, Caillies S (2016) Neural correlates of contrast and humor: processing common features of verbal irony. *PLoS ONE* 11(11):e0166704. <https://doi.org/10.1371/journal.pone.0166704>
- Olano MA, Acevedo BE, Chambeaud N, Acuña A, Marcó M, Kochen S, Alba-Ferrara L (2020) Emotional salience enhances intelligibility in adverse acoustic conditions. *Neuropsychologia* 147:107580. <https://doi.org/10.1016/j.neuropsychologia.2020.107580>
- Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9(1):97–113. [https://doi.org/10.1016/0028-3932\(71\)90067-4](https://doi.org/10.1016/0028-3932(71)90067-4)
- Parola A, Gabbatore I, Bosco FM, Bara BG, Cossa FM, Gindri P, Sacco K (2016) Assessment of pragmatic impairment in right hemisphere damage. *J Neurolinguistics* 39:10–25. <https://doi.org/10.1016/j.jneuroling.2015.12.003>
- Paunov A (2018) *fMRI studies of the relationship between language and theory of mind in adult cognition* [Doctoral Thesis, Massachusetts Institute of Technology.]. MIT Libraries. <https://dspace.mit.edu/handle/1721.1/121828>
- Pexman PM, Glenwright M (2007) How do typically developing children Grasp the meaning of verbal Irony?? *J Neurolinguistics* 20(2):178–196. <https://doi.org/10.1016/j.jneuroling.2006.06.001>
- Phan KL, Wager T, Taylor SF, Liberzon I (2002) Functional neuroanatomy of emotion: A Meta-Analysis of emotion activation studies in PET and fMRI. *NeuroImage* 16(2):331–348. <https://doi.org/10.1006/nimg.2002.1087>
- Rankin KP, Salazar A, Gorno-Tempini ML, Sollberger M, Wilson SM, Pavlic D, Stanley CM, Glenn S, Weiner MW, Miller BL (2009) Detecting sarcasm from paralinguistic cues: anatomic and cognitive correlates in neurodegenerative disease. *NeuroImage* 47(4):2005–2015. <https://doi.org/10.1016/j.neuroimage.2009.05.077>
- Rapp AM, Mutschler DE, Wild B, Erb M, Lengsfeld I, Saur R, Grodd W (2010) Neural correlates of irony comprehension: the role of schizotypal personality traits. *Brain Lang* 113(1):1–12. <https://doi.org/10.1016/j.bandl.2009.11.007>
- Rapp AM, Mutschler DE, Erb M (2012) Where in the brain is nonliteral Language?? A coordinate-based meta-analysis of functional magnetic resonance imaging studies. *NeuroImage* 63(1):600–610. <https://doi.org/10.1016/j.neuroimage.2012.06.022>
- Rapp AM, Langohr K, Mutschler DE, Klingberg S, Wild B, Erb M (2013) Isn't it ironic? Neural correlates of irony comprehension in schizophrenia. *PLoS ONE* 8(9):e74224. <https://doi.org/10.1371/journal.pone.0074224>
- Reyes-Aguilar A, Valles-Capetillo E, Giordano M (2018) A quantitative Meta-analysis of neuroimaging studies of pragmatic Language comprehension: in search of a universal neural substrate. *Neuroscience* 395(March 2020):60–88. <https://doi.org/10.1016/j.neuroscience.2018.10.043>
- Ross RS, Slotnick SD (2008) The hippocampus is preferentially associated with memory for Spatial context. *J Cogn Neurosci* 20(3):432–446. <https://doi.org/10.1162/jocn.2008.20035>
- Schurz M, Radua J, Aichhorn M, Richlan F, Perner J (2014) Fractionating theory of Mind: A meta-analysis of functional brain imaging studies. *Neurosci Biobehavioral Reviews* 42:9–34. <https://doi.org/10.1016/j.neubiorev.2014.01.009>
- Shamay-Tsoory SG, Tomer R, Aharon-Peretz J (2005) The neuroanatomical basis of Understanding sarcasm and its relationship to social cognition. *Neuropsychologia* 19(3):288–300. <https://doi.org/10.1037/0894-4105.19.3.288>
- Shibata M, Abe J, Terao A, Miyamoto T (2007) Neural mechanisms involved in the comprehension of metaphoric and literal sentences: an fMRI study. *Brain Res* 1166(1):92–102. <https://doi.org/10.1016/j.brainres.2007.06.040>

- Slotnick SD, Schacter DL (2004) A sensory signature that distinguishes true from false memories. *Nat Neurosci* 7(6):664–672. <https://doi.org/10.1038/nn1252>
- Spotorno N, Koun E, Prado J, Van Der Henst J-B, Noveck IA (2012) Neural evidence that utterance-processing entails mentalizing: the case of irony. *NeuroImage* 63(1):25–39. <https://doi.org/10.1016/j.neuroimage.2012.06.046>
- Tsolakopoulos D, Kasselimis D, Laskaris N, Angelopoulou G, Papa-georgiou G, Velonakis G, Varkanitsa M, Tountopoulou A, Vasilopoulou S, Goutsos D, Potagas C (2023) Exploring pragmatic deficits in relation to theory of Mind and executive functions: evidence from individuals with right hemisphere stroke. *Brain Sci* 13(10):1385. <https://doi.org/10.3390/brainsci13101385>
- Uchiyama H, Seki A, Kageyama H, Saito DN, Koeda T, Ohno K, Sadato N (2006) Neural substrates of sarcasm: A functional magnetic-resonance imaging study. *Brain Res* 1124(1):100–110. <https://doi.org/10.1016/j.brainres.2006.09.088>
- Uchiyama H, Saito DN, Tanabe HC, Harada T, Seki A, Ohno K, Koeda T, Sadato N (2012) Distinction between the literal and intended meanings of sentences: A functional magnetic resonance imaging study of metaphor and sarcasm. *Cortex* 48(5):563–583. <https://doi.org/10.1016/j.cortex.2011.01.004>
- Valles-Capetillo E, Ibarra C, Martinez D, Giordano M (2022) A novel task to evaluate irony comprehension and its essential elements in Spanish speakers. *Front Psychol* 13(November):1–18. <https://doi.org/10.3389/fpsyg.2022.963666>
- Varga E, Simon M, Tényi T, Schnell Z, Hajnal A, Orsi G, Dóczi T, Komoly S, Janszky J, Füredi R, Hamvas E, Fekete S, Herold R (2013) Irony comprehension and context processing in schizophrenia during remission— A functional MRI study. *Brain Lang* 126(3):231–242. <https://doi.org/10.1016/j.bandl.2013.05.017>
- Wang AT, Lee SS, Sigman M, Dapretto M (2006a) Neural basis of irony comprehension in children with autism: the role of prosody and context. *Brain* 129(4):932–943. <https://doi.org/10.1093/brain/awl032>
- Wang AT, Lee SS, Sigman M, Dapretto M (2006b) Developmental changes in the neural basis of interpreting communicative intent. *Soc Cognit Affect Neurosci* 1(2):107–121. <https://doi.org/10.1093/scan/nsi018>
- Williams DL, Cherkassky VL, Mason RA, Keller TA, Minshew NJ, Just MA (2013) Brain function differences in Language processing in children and adults with autism. *Autism Res* 6(4):288–302. <https://doi.org/10.1002/aur.1291>
- Winner E, Gardner H (1993) Metaphor and irony: Two levels of understanding. In *Metaphor and Thought* (Issue c, pp. 425–444). Cambridge University Press. <https://doi.org/10.1017/CBO9781139173865.021>
- Woodland J, Voyer D (2011) Context and intonation in the perception of sarcasm. *Metaphor Symbol* 26(3):227–239. <https://doi.org/10.1080/10926488.2011.583197>

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