

What is the difference between irony and sarcasm? An fMRI study

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Abstract

Verbal irony is a figure of speech that communicates the opposite of what is said, while sarcasm is a form of irony that is directed at a person, with the intent to criticise. The current study used functional magnetic resonance imaging (fMRI) with the aim of mapping the neural networks involved in the processing of sarcastic and non-sarcastic irony. Participants read short texts describing an interaction between two characters, which ended in either a literal, sarcastic, or non-sarcastic ironic comment. Results showed that the mentalising network (mPFC) and semantic network (IFG) were more activated for non-sarcastic irony than for literal controls. This would suggest that interpreting this kind of language involves understanding that the speaker does not mean what they literally say, as well as processes involved in conflict detection and resolution. Sarcastic irony recruited more of the semantic network, as well as areas associated with humour appreciation and subcortical structures, indicating that more complex neural mechanisms underlie the comprehension of sarcastic versus non-sarcastic irony.

Keywords: irony; sarcasm; fMRI; theory of mind; humor

1. Introduction

The conventional view of verbal irony is that it is a figure of speech that communicates the opposite of what is said (Grice, 1975). For example, by saying “What lovely weather” in the middle of a storm, the speaker actually communicates “What terrible weather”. Sarcasm is a form of irony that, as well as communicating the opposite of what is said, is generally directed at a person with the intent to be critical (e.g., Kreuz & Glucksberg, 1989, Matsui et al., 2016; Shamay-Tsoory, Tomer, & Peretz, 2005). An example of sarcasm would be a comment such as “That was clever” being uttered in a context in which the target of the comment has done something stupid. Although both sarcastic and non-sarcastic irony involve computation of what the speaker actually intends to say (which mismatches with context), the comprehension of sarcastic irony may also involve an emotional component. Thus, the aim of the current paper is to investigate the neural substrates involved in the comprehension of sarcastic and non-sarcastic irony.

Researchers suggest that the successful comprehension of irony depends on the perceiver’s ability to infer other people’s mental states, thoughts, and feelings (Channon, Pellijeff, & Rule, 2005). Thus, we would anticipate that the comprehension of both sarcastic and non-sarcastic irony should involve brain areas specialised in social cognition, since in both cases the participant must calculate that the intended message is different from the literal one. Specifically, we might expect activation of the “mentalising network”, which is a system of brain areas that are known to be involved in mentalising processes. These processes include attributing mental states to other people, understanding their intentions, understanding that they can hold either true or false beliefs about reality, and being able to predict their future behaviour

based on their beliefs. Reviews of the literature suggest that the mentalising network involves the medial prefrontal cortex (mPFC), the temporo-parietal junction (TPJ), and the posterior superior temporal sulcus (STS), as well as parts of the posterior cingulate cortex and precuneus (e.g., Frith & Frith, 2006). In support of this, more recent meta-analyses also indicate that the mentalising network includes the mPFC and the bilateral posterior TPJ (Schurz, Aichhorn, Richlan, & Perner, 2014; van Overwalle & Baetens, 2009).

A number of studies investigating the brain regions involved in the interpretation of irony have supported the assumption that irony comprehension recruits the mentalising network. For example, in a lesion study, Shamay-Tsoory et al. (2005) compared three groups of participants: healthy controls, patients with lesions to the PFC (which is part of the mentalising network), and those with lesions to the posterior cortex (which is not). Patients with PFC lesions made significantly more mistakes when interpreting sarcastic comments when compared to both other groups (who had intact performance). Patients with PFC lesions also presented impairments in their theory of mind ability, which correlated with their sarcasm comprehension deficit. These results support the proposition that successful comprehension of sarcasm is not possible in the absence of mentalising abilities.

In line with this proposal, more recent evidence from brain imaging studies has consistently showed activation in parts of the mentalising network during irony comprehension (e.g., Eviatar & Just, 2006; Rapp et al., 2010; Shibata, Toyomura, Itoh, & Abe, 2010; Spotorno, Koun, Prado, Van Der Henst, & Noveck, 2012; Wakusawa et al., 2007; Wang, Lee, Sigman, & Dapretto, 2006). To bring together findings in this area, Rapp, Mustshcler, and Erb (2012) conducted a meta-analysis of fMRI studies of figurative language comprehension. From their findings, they note

that the mPFC plays a role in non-literal language comprehension, in particular for irony. This further supports the suggestion that the mentalising network underpins the successful comprehension of this kind of language. Results from a similar meta-analysis of neuroimaging studies of figurative language comprehension conducted by Bohrn, Altmann, and Jacobs (2012) also support the conclusion that the mPFC is more involved in irony comprehension than in the comprehension of other types of figurative language such as metaphor and idiom, for which mentalising operations are less important.

In addition to activation of the mentalising network, the meta-analysis of Rapp et al. (2012) showed that the inferior frontal gyrus (IFG, in particular Brodmann Areas (BA) 47 and 45) plays a key role in the comprehension of non-literal language. They suggested that this might reflect the greater demands involved in contextual integration of non-literal versus literal language, or selection between competing literal versus non-literal interpretations. Rapp et al. reported that this activation extended from BA47/45 to other parts of the IFG (including Broca's area), as well as the insula, BA9, parts of the left lateral prefrontal cortex (BA6 and 46), and the inferior parietal lobule (BA39). They concluded from this that these regions formed a network in the left hemisphere that plays a key role in the comprehension of non-literal meaning. Studies conducted subsequently to these meta-analyses also consistently show activation of semantic networks and theory of mind networks during irony comprehension (see e.g., Akimoto et al., 2014; Bosco, Parola, Valentini, & Morese, 2017; Obert et al., 2016).

Sarcasm has been used as a synonym for irony in many research papers, but given the differences in the social and emotional functions of sarcastic versus non-sarcastic irony, it is important to explore differences in the brain mechanisms

underlying the way in which they are understood. Shamay-Tsoory et al. (2005) studied sarcasm, specifically. In their lesion study, patients with damage to the right hemisphere had profound deficits in emotion recognition, whereas those with right prefrontal damage, especially to the ventromedial (VM) regions, had problems with theory of mind tasks. Both of these abilities were related to the patients' poor understanding of sarcasm (Shamay-Tsoory et al., 2005). These results suggest that we might expect to observe brain areas involved in affective processing being activated during sarcasm comprehension. However, it is currently unknown whether such areas are involved in the processing of both sarcastic and non-sarcastic irony. This question would benefit from converging evidence from healthy adults using functional imaging methods.

A number of recent brain imaging studies have focused on sarcasm, specifically. For example, Uchiyama et al. (2006) studied sarcasm comprehension and concluded that the neural substrates of sarcasm include; the left temporal pole, the STS, the mPFC, and the IFG (see also Matsui et al. 2016 for recent supporting evidence that the IFG, in particular, BA47, may be crucial for sarcasm comprehension). However, in Uchiyama et al.'s study the contrast was not made between the comprehension of sarcastic and literal language, but between the brain regions activated during both sarcastic and literal conditions compared to those activated when reading a sentence unconnected to the context. Uchiyama et al. (2012) compared sarcasm and metaphor comprehension and found that both involve the activation of the anterior-rostral MFC (which is essentially the same as the VM-PFC, BA10). Therefore, these studies seem to support Shamay-Tsoory et al.'s (2005) proposition that the VM-PFC plays an important role in the comprehension of sarcastic ironies.

In relation to social and emotional processing specifically, Uchiyama et al. (2012) found that the left amygdala was also activated in their sarcasm comprehension task. They hypothesised that this was because the amygdala is associated with inferring the emotional state of an individual, which is a necessary step in the correct processing of a sarcastic comment (but may be less crucial for non-sarcastic irony; no amygdala activation is reported for studies of irony covered by the meta-analyses of Bohrn et al., 2012, and Rapp et al., 2012). In support of this, Akimoto et al. (2014) also report modulation of activity in the right amygdala depending on the degree of irony (or 'hiniku', which is more akin to sarcasm) that was perceived by participants in relation to sarcastic stimuli. Thus, we can conclude that the amygdala may play a role in the emotional processing of this form of language, which is a reasonable assumption given that amygdala activation is known to be modulated by emotional arousal (Zald, 2003).

From the discussion above, it is clear that although some studies have focused specifically on sarcasm (e.g., Matsui et al., 2016; Shamay-Tsoory et al., 2005; Uchiyama et al., 2006; 2012), most other studies do not distinguish between sarcastic and non-sarcastic irony (with experimental materials generally comprising a mixture of the two). Thus, it is currently unclear whether the same neural mechanisms are recruited during the processing of sarcastic versus non-sarcastic irony.

Further reasons to anticipate differences in the neural mechanisms underlying the comprehension of sarcastic versus non-sarcastic irony arise from insights from the developmental literature. Specifically, according to Pexman and Glenwright (2007), sarcasm comprehension is said to require two skills: (1) recognising that the speaker does not believe what they literally say (which is required to understand both sarcastic and non-sarcastic irony) and (2) recognising that the speaker's intention is to be

critical (in the case of negative sarcastic ironies) or make a compliment (in the case of positive sarcastic ironies). These two skills develop at different stages. Assessing a speaker's belief requires first-order mental state reasoning which is attained by children around the age of four. Assessing a speaker's intent requires second-order mental state reasoning which is usually mastered after six years of age (Frith & Frith, 2003).

This may suggest that non-sarcastic ironic comments can be understood by children after the age of four, but sarcastic comments can only be fully understood after the age of six, when second-order reasoning has been developed. Evidence in support of this claim comes from Glenwright and Pexman (2010). They found that as expected, five to six-year olds understand that the speaker of an ironic or a sarcastic comment actually means the opposite of what they say. However, only nine to 10-year olds were able to also understand the intentions of the sarcastic speaker by rating sarcastic criticism as more "mean" than ironic criticism. Therefore, children do not seem to distinguish between irony and sarcasm until the age of nine or 10, when they master second-order mental state reasoning. This conclusion is also supported by a review of the research conducted with children into understanding non-literal forms of language (Creusere, 1999). Thus, although it is clear that mentalising processes underlie the comprehension of both sarcastic and non-sarcastic irony, it may be the case that more complex processes are involved in the interpretation of sarcastic irony due to the increased demands involved in assessing speaker intention as well as speaker belief.

1.1 The current study

In the current study, we use fMRI to investigate the neural mechanisms underlying the processing of sarcastic and non-sarcastic irony. Participants will be presented with short written scenarios that conclude with sarcastic irony, non-sarcastic irony, or literal utterances made by one of the characters. We will use an event-related fMRI design to identify the brain regions activated during comprehension of those utterances.

Based on results from the studies presented above, we make the following predictions: Firstly, following the assumption that the mentalising network is involved in the processing of irony, and the supporting findings that areas of the mentalising network (in particular, the mPFC) are activated during the comprehension of irony, we would expect to observe higher activation in the mPFC for both sarcastic and non-sarcastic ironies, compared to literal controls. Secondly, following the meta-analysis of Rapp et al. (2012), which showed that the IFG plays a key role in the comprehension of non-literal language, we would also expect to see greater activation in the IFG (in particular BA47 and 45) for both sarcastic and non-sarcastic ironies, compared to literal controls. This would reflect the greater demands involved in contextual integration for ironic materials, or selection between competing literal versus ironic interpretations. Furthermore, based on the assumption that the comprehension of sarcastic irony requires more complex mentalising processes than non-sarcastic irony (e.g., Pexman & Glenwright, 2007), we may expect more activation in the mentalising network during the comprehension of sarcastic irony. In addition, since sarcasm carries more emotional connotations than non-sarcastic irony (due to the additional element of personal criticism), we may predict greater activation in the emotional network for sarcastic ironies than non-sarcastic ironies.

Specifically, we may also expect greater activation in the left (Uchiyama et al., 2012) or right (Akimoto et al., 2014) amygdala for sarcastic ironies.

2. Method

2.1 Participants

The study was approved by the ethics committee of the Faculty of Medicine and Health Sciences at the University of Nottingham. Seventeen participants (seven males) were recruited from the University of Nottingham community (the meta-analysis of Rapp et al., 2012, reported that fMRI studies of non-literal language have an average of 15.4 participants). Participants were aged between 19-29 years old ($M = 24$). All participants confirmed that they were right-handed, were native English speakers with normal or corrected to normal vision, had no reading disabilities, and no history of mental or neurological illness. All participants gave written informed consent, and received an inconvenience allowance of 10 pounds for taking part.

2.2 Materials and design

Sixty short stories, or scenarios, were created, each consisting of a dialogue between two characters (see Table 1 for an example, and supplementary materials for the full set). The first two sentences of each scenario were the same across conditions and simply introduced the two characters (e.g., “Bernice and Caitlin were both applying for a Psychology course at a university in the USA. They went to print out their applications together.”). The third sentence differed between conditions (sarcastic irony, non-sarcastic irony, and literal). In the sarcastic irony condition the third sentence set up a situation (e.g., “Caitlin chose to print hers on pink paper.”) that was designed to lead to the final comment (“Very formal!”) being interpreted as a

criticism directed at one of the characters (in this case, Caitlin). In contrast, in the non-sarcastic irony condition the third sentence set up a situation (e.g., “The printer only had pink paper available.”) that was designed to lead to the final comment being interpreted as an ironic comment on the situation, and not a criticism of the character. In the literal condition, the third sentence (e.g., “Caitlin chose to print hers on letter headed paper.”) set up a situation designed to lead to the final comment being interpreted literally (and not as criticism).

In addition to the experimental materials, there were 20 filler items. The filler items also contained a short dialogue between two characters, ending in a target utterance that was intended to be interpreted as literal criticism (e.g., “I thought it would be more interesting!”) when the context was also negative (e.g., The lecture was so boring that the character fell asleep). This was to prevent participants from building up an expectation for an ironic target sentence following a negative event in the context.

Table 1. Example scenario in all three conditions, plus example filler item.

<i>Sarcastic irony</i>	Bernice and Caitlin were both applying for a Psychology course at a university in the USA. They went to print out their applications together. Caitlin chose to print hers on pink paper. Bernice said to Caitlin: “Very formal!”
<i>Non-sarcastic irony</i>	Bernice and Caitlin were both applying for a Psychology course at a university in the USA. They went to print out their applications together. The printer only had pink paper available. Bernice said to Caitlin: “Very formal!”
<i>Literal</i>	Bernice and Caitlin were both applying for a Psychology course at a university in the USA. They went to print out their applications together. Caitlin chose to print hers on letter headed paper. Bernice said to Caitlin: “Very formal!”
<i>Filler</i>	Jade went with Sabrina to one of her lectures on marine biology. She was interested in the topic in general, however, the lecture was so boring that Sabrina fell asleep half way through. Sabrina said to Jade: “I thought it would be more interesting!”

Materials were counterbalanced across three separate stimulus presentation files so that each participant only saw one version (sarcastic irony, non-sarcastic irony, or literal) of each experimental item. Thus, each participant read 80 short stories in total (20 sarcastic irony, 20 non-sarcastic irony, 20 literal, and 20 filler items), presented in a random order.

2.3 Procedure

PsychoPy (Peirce, 2007) was used to visually present the stimuli on a screen, which each participant read from a mirror from within the scanner. For each scenario, participants first read the context, which consisted of the entire text up to the target utterance. This context was displayed for a 15s period to give all participants enough time to read the entire text. A fixation cross followed, and was displayed for 2.5s. Then the target utterance (e.g., “Very formal!”) was displayed for 2.5s, which was followed by another fixation cross for 5s. Participants were then presented with a comprehension question which asked them to indicate whether the final comment was ironic or not. They pressed one of two buttons to answer either: “Yes” the final comment was ironic, or “No” the final comment was not ironic (see Figure 1 for an illustration of the trial sequence). Participants were instructed to read at their normal rate, and to respond as accurately as possible to the questions.

Each session started with six practice scenarios, in order to familiarise participants with the task. This practice run was followed by four runs of 20 scenarios. The participants were able to briefly rest between runs, and also during the anatomical image acquisition that took place between the second and third runs. A typical session in the scanner lasted about 40 minutes in total.

Since the task involved participants having to take the perspective of

characters in text rather than interpreting comments that were directed at themselves, we considered it important to take into account whether or not participants had the ability to take the perspective of the story characters when interpreting the comments. Thus, we took a measure of their perspective taking abilities, which could then be entered into the analyses.¹ Specifically, following scanning, participants completed the Interpersonal Reactivity Index (IRI) (Davis, 1980), which is a measure of empathy. The IRI has four subscales: (1) the perspective-taking scale assesses the respondent's ability to see things from another person's point of view, (2) the fantasy scale measures the tendency to identify with fictional characters in movies, plays etc., (3) the empathic concern scale assesses one's feelings of compassion for others, and finally (4) the personal distress scale measures the respondent's feelings of discomfort following the observation of somebody else's distress or negative experience. Shamay-Tsoory, Aharon-Peretz, and Perry (2009) considered two separate systems for empathy: one that is a simple emotion contagion system, and one that represents cognitive perspective-taking. In their study, they took the mean score of the perspective-taking and fantasy scale subscales of the IRI as a measure of cognitive empathy, and thus that is the approach we will adopt here.

2.4 MRI acquisition

The functional and anatomical images were acquired at the University of Nottingham's Sir Peter Mansfield Imaging Centre on a Phillips 3.0T scanner, using a Phillips SENSE 32-channel parallel head coil. T1-weighted anatomical images were acquired using a standard MP-RAGE sequence (240x240x160, 1x1x1mm³ voxels, 8° flip angle, TR = 8.4ms, TE = 3.9ms). The functional images were acquired using a double-echo pulse sequence (80x80x35, 3x3x3mm³ voxels, 8° flip angle, TR = 2.5s,

$TE_1 = 20\text{ms}$, $TE_2 = 45\text{ms}$).

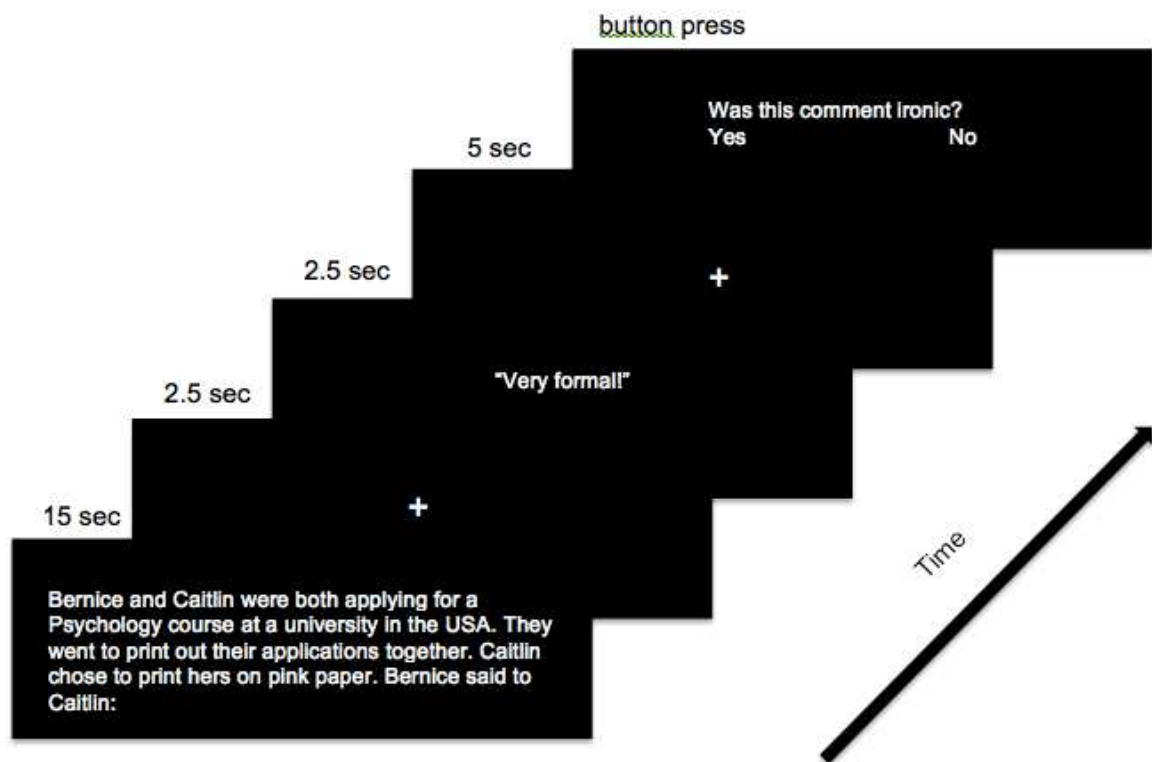


Figure 1. Illustration of the trial sequence.

2.5 fMRI analysis

The fMRI data were analysed using SPM12 (<http://www.fil.ion.ucl.ac.uk/spm>). For each participant, the functional images were first corrected for slice acquisition delays and spatially realigned to the first image in the session to correct for head movements. The motion-corrected images were then co-registered to their associated anatomical scans and spatially normalised into standard MNI (Montreal Neurological Institute) space. Finally, they were smoothed with an 8mm full-width at half maximum, isotropic Gaussian kernel.

A mixed-effect, event-related statistical analysis was performed using SPM12's standard two-level general linear model approach. For each participant, the

time series were first high-pass filtered at 1/128 Hz and corrected for serial correlations with an autoregressive AR (1) model. Event-related signal changes were estimated at each voxel by modeling the appearance of the target sentences as delta functions convolved with the standard SPM hemodynamic response function combined with time derivatives. We also modeled the context stories and the comprehension questions separately, and excluded trials for which the participant's answer to the latter was incorrect. At the second level, one-sample t-tests were performed on the parameter estimates pertaining to the target sentence regressor, with, as a covariate, the mean of participants' scores from the perspective-taking and fantasy subscales from the IRI (which we use as measure of cognitive empathy following Shamay-Tsoory et al., 2009). Paired t-tests were also performed to contrast (Sarcastic Irony - Literal) against (Non-sarcastic Irony - Literal), which is equivalent to Sarcastic Irony against Non-sarcastic Irony. In line with the recommendations of Lieberman and Cunningham (2009) we report the activations that survived a whole brain uncorrected threshold of $p < 0.005$ with minimum cluster size of 20 voxels. Activations are given in terms of MNI coordinates, in terms of anatomic labels, and in terms of Brodmann Areas (BA), as determined from the MNI coordinates using the Yale BioImage Suite Package, with the BAs defined in MNI space according to Lacadie, Fulbright, Arora, Constable, and Papademetris (2008). In line with the recommendations of Devlin and Poldrack (2007), we also report (when available) probabilistic BA estimates obtained using the Juelich's probabilistic BA maps (Zilles et al., 1995) in order to explicitly take into account natural anatomical variability.

3. Results and Discussion

Behavioural data

We first report accuracy and response time data (see Table 2 for descriptive statistics). Accuracy data accords to cases in which a participant correctly classified ironic and sarcastic utterances as irony, and correctly classified literal items as being non-ironic. Response time data indicates the time taken from the question (“Was this comment ironic?”) appearing on the screen, to the participant pressing a button to indicate their response.

Table 2. Accuracy and response time data.

Measure	Literal		Sarcastic Irony		Non-sarcastic Irony	
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
Accuracy (% correct)	96.0	5.8	95.3	6.4	96.3	8.9
Response time (msec)	897	43.9	920	41.4	931	41.4

Accuracy: All participants scored on average 85% correct or above, with the percentage of correct responses ranging from 85% to 100%. Thus, all participants were shown to have engaged in the task and understood the scenarios. There were no significant differences in accuracy between conditions ($F1 < 1$; $F2 < 1$).

Response times: Response times were calculated for correct responses only (4.2% of data removed). Responses below 150 ms (0.8 %) and above 5 seconds (0.3 %) were also removed. There were no significant differences in response times between conditions ($F1 < 1$; $F2 < 1$).

fMRI data

We will start by discussing brain regions that show more activation for non-sarcastic ironic materials than for literal materials (Non-sarcastic Irony > Literal contrast) and for sarcastic irony compared to literal materials (Sarcastic Irony > Literal contrast). We will then discuss differences that were observed between sarcastic and non-sarcastic irony (Sarcastic Irony > Non-sarcastic Irony contrast). We

did not find activations for Literal > Sarcastic irony, Literal > Non-sarcastic irony, or Non-sarcastic Irony > Sarcastic Irony, which provides evidence in support of the specificity of the activations found for irony and sarcasm.

3.1 Non-sarcastic Irony > Literal

For non-sarcastic irony compared to literal materials, we firstly predicted greater activation in the mentalising network, in particular the mPFC. In support of this prediction, results of Non-sarcastic irony > Literal showed greater activity in regions of the mPFC, specifically, BA10 (left and right). We also predicted more activation in the IFG, in particular BA47 and 45 (following Rapp et al., 2012). Again, in support of our predictions, results of Non-sarcastic irony > Literal showed greater activity in the IFG, specifically, BA47 (right) (see Table 3 and Figure 2 for details).

These results are in line with previous findings in the literature suggesting that the mentalising network, in particular the mPFC, are important for the comprehension of irony (see e.g., Bohrn et al., 2012; Rapp et al., 2012, for overviews). That is, greater activation of the mPFC for ironic than literal materials suggests greater involvement of the mentalising network in interpreting ironic than literal comments. This fits with the suggestion that the comprehension of irony involves recognising that the speaker does not believe what they literally say (e.g., Pexman & Glenwright, 2007).

In addition, greater activation of BA47, which is part of the IFG, is also in line with findings from previous brain imaging studies, and suggests that understanding irony involves greater effort in contextual integration, or selection between competing literal versus ironic interpretations (again see e.g., Rapp et al. 2012, for an overview, and e.g., Akimoto et al., 2014; Obert et al., 2016, for more recent discussions). Such a

finding supports the theoretical perspective that the successful comprehension of irony relies on activating both the literal and ironic meaning of an utterance, in order that the difference between them can be represented. This underlines the function of irony as highlighting the difference between what is expected or desirable in a situation (i.e., the literal interpretation), and reality (the ironic one, see Giora 1995, see also Filik, Wallington, Leuthold, & Page, 2014, for further empirical evidence). Importantly, we would expect this process to underlie comprehension of both sarcastic and non-sarcastic irony.

As well as supporting previous findings, the current results also add to our knowledge in this area. Specifically, previous brain imaging studies have either examined sarcasm alone (e.g., Matsui et al., 2016; Uchiyama et al., 2006; 2012), or have included materials that are a mixture of sarcastic and non-sarcastic irony. Here, we have provided novel evidence that the mPFC and IFG are important for processing non-sarcastic irony, which may arguably be less complex than processing sarcasm (e.g., Glenwright & Pexman, 2010; Pexman & Glenwright 2007).

Table 3: Coordinates, cluster extent, peak Z-scores and anatomical names of the supra-threshold clusters.

Anatomical location	Brodmann Area (BA)	Probabilistic Anatomy (Juelich atlas)	MNI coordinates (x, y, z)	Z-score (peak)	Cluster extent (pixels)
Non-sarcastic Irony > Literal					
Pre-frontal cortex	Right BA10	---	(22, 50, -8)	4.39	70
	Right BA47	---	(30, 44, -12)	3.13	
	Left BA10	---	(-34, 46, -2)	3.58	183
Sarcastic Irony > Literal					
Frontal cortex	Left BA9	Left BA44 (18%), Left BA45 (16%)	(-52, 22, 36)	3.89	330

	Left BA46	Left BA45 (63%), Left BA44 (10%)	(-48, 32, 22)	3.39	
	Right BA8	---	(38, 20, 32)	3.40	44
	Right BA9	---	(46, 22, 34)	3.13	
Pre-frontal cortex	Left BA10	---	(-28, 54, 0)	2.93	38
Parietal cortex	Left BA39 (Yale), Left BA40 (WFU)	Left Inferior parietal lobule Pfm (40%), Pga (40%), PF (17%), Left Alocat anterior intra-parietal sulcus hIP1 (4%), hIP2 (10%), hIP3 (5%),	(-48, -52, 36)	2.78	21
(Sarcastic Irony - Literal) > (Non-sarcastic Irony - Literal), i.e., Sarcastic Irony > Non-sarcastic Irony					
Frontal cortex	Right BA6	Right Inferior parietal lobule Pfm (31%)	(8, 10, 56)	3.71	134
	Right BA6	Right BA6 (10%)	(16, 12, 56)	3.31	
Basal ganglia	Putamen	Left Corticospinal tract (19%)	(-26, -2, 16)	3.42	93
Frontal cortex	Right BA6	---	(36, 4, 54)	3.30	49
Cerebellum	Cerebellum	---	(-4, -40, -10)	3.52	22

3.2 Sarcastic Irony > Literal

For sarcastic irony compared to literal materials, we also predicted more activation in the mPFC and IFG, as for non-sarcastic irony. Firstly, in relation to our prediction of greater activation in the mPFC, results of Sarcastic Irony > Literal showed greater activation in both BA9 (left and right) and BA10 (left), which are all part of the mPFC. Interestingly, more of the mentalising network was activated for sarcastic irony than for non-sarcastic irony (when both are compared to literal controls). This would fit with the previously discussed proposal from Pexman and Glenwright (2007) that more complex mentalising operations are required for the successful comprehension of sarcastic irony than for non-sarcastic irony. Specifically, for both types of irony, the listener must compute that the speaker does not believe

what they are literally saying, but for sarcastic irony the listener must also calculate speaker intent or social purpose in making the comment (i.e., to criticise).

It is useful at this point to consider further specificity when examining the PFC regions that are activated by sarcastic and non-sarcastic irony, in comparison to literal controls. In looking at Figure 2, we can see different distributions of activity for non-sarcastic (panel a) compared to sarcastic irony (panel b). Specifically, PFC activation in sarcastic irony appears to be more caudal in focus than for non-sarcastic irony. This is an interesting finding in light of meta-analyses showing a gradation in function across certain areas of the PFC, in particular, BA10, which is activated in both comparisons here. In particular, Gilbert et al. (2006) noted variations in function across a rostral-caudal axis, with studies involving mentalizing reporting more caudal activation. Furthermore, other studies (e.g., Brunet, Sarfati, Hardy-Baylé, & Decety, 2000) report activation for BA9 for tasks involving the attribution of intentions to others, with instead more rostral PFC activation for judgements relating to the self (e.g., Denny, Kober, Wager, & Ochsner, 2012). Thus, it would appear that the activation of more caudal regions for sarcastic irony may be the result of participants making other-related mentalizing judgments about the materials at hand, specifically, in calculating speaker intent (i.e., intent to criticize).

It is important to note that the meta-analysis that Rapp et al. (2012) conducted on fMRI studies of figurative language found that most of the reported evidence of activity in the mPFC came from research on irony. However, there was also some evidence for the involvement of this region in the processing of metonymy, metaphor, and idioms (which are not generally associated with theory of mind-related operations). Thus, it should be acknowledged that activation in the mPFC could also be indicative of other processes involved in the comprehension of figurative language,

such as the suppression of alternative interpretations (see e.g., Papagno & Romero-Lauro, 2010).

In terms of our predictions for increased activation in the IFG for sarcastic compared to literal materials, the results showed greater activation in BA45 (left) and BA44 (left). This finding, in particular the activation in BA45, would support the findings of previous studies (see e.g., Rapp et al., 2012, for discussion), and would suggest that sarcastic irony, like non-sarcastic irony, involves more complex contextual integration processes than literal language. It also may require the representation of both the literal and sarcastic meanings of the utterance. Note that although Rapp et al. stated that the primary regions for IFG activation would be BA45 and 47, they noted that this activation extended from BA47/45 to other parts of the IFG (including Broca's area), as well as the insula, BA9, parts of the left lateral prefrontal cortex (BA6 and 46), and the inferior parietal lobule (BA39); a number of which were found to be activated in the current contrast (see Table 3).

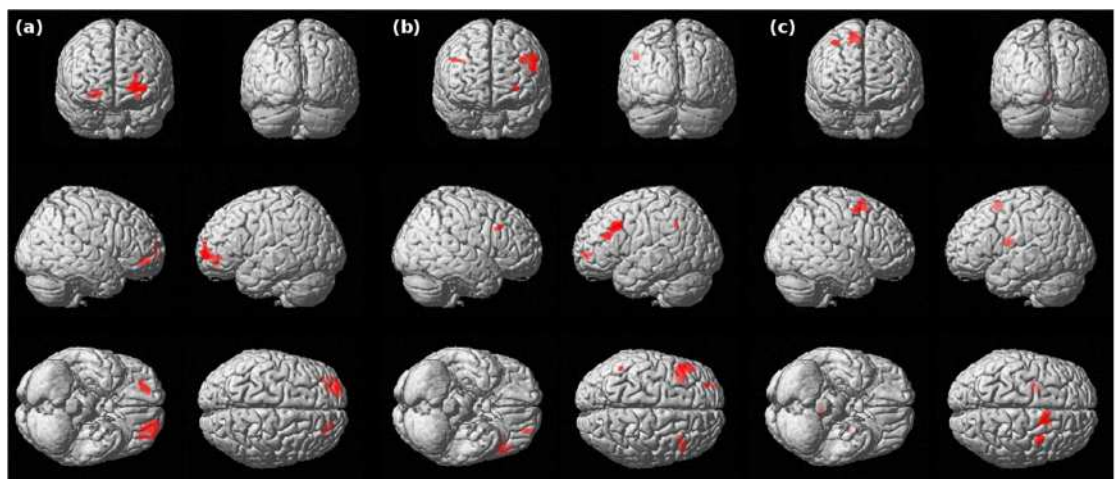


Figure 2: Regions exhibiting significant activation for the following contrasts:

(a) Non-sarcastic Irony > Literal, (b) Sarcastic Irony > Literal, (c) (Sarcastic Irony - Literal) > (Non-sarcastic Irony - Literal).

To place the current results in a wider context, we consider at this point why someone might use sarcasm to criticise another individual (or indeed to use non-sarcastic irony), rather than using literal language. This is of particular interest given that the use of figurative expressions may result in misunderstanding and increased processing effort required on the part of the receiver. Some researchers have argued that the use of irony and sarcasm can fulfill certain socio-emotional functions, whether it is to be humorous (e.g., Colston & Keller, 1998; Colston & O'Brien, 2000; Filik, Brightman, Gathercole, & Leuthold, 2017; Kreuz, Long, & Church, 1991; Kumon-Nakamura, Glucksberg, & Brown, 1995; Obert et al., 2016; Roberts & Kreuz, 1994), aggressive (e.g., Blasko & Kazmerski, 2006), to appear emotionally controlled (e.g., Dews, Kaplan, & Winner, 1995), or to ridicule, mock, or tease (e.g., Clark & Gerrig, 1984, Kreuz et al., 1991; Pexman & Zvaigzne, 2004). Since humour is one of the main themes to emerge in the literature, we now discuss our findings in relation to brain regions that are involved in humour comprehension.

In a recent review of fMRI studies examining humour comprehension, Vrticka, Black, and Reiss (2013) argue that humour comprehension engages two networks of brain areas. Firstly, there are brain regions that are associated with 'cognitive' components of humour comprehension. In particular, Vrticka et al. note that the cognitive component of humour comprehension relies on the activation of language and semantic processing areas such as the (left) IFG (BA45, BA46, and BA47) and the temporal pole (TP, BA38). They argued that other areas involved in the cognitive component of humour comprehension are those involved in incongruity detection and resolution (TPJ, BA22, BA39, and BA40). They further note that if the stimuli require theory of mind, then humour comprehension will also recruit

associated areas such as the mPFC, posterior cingulate cortex (PCC), precuneus (PREC), as well as the anterior and superior STG (superior temporal gyrus) and STS. It is apparent from this that many of the brain regions recruited during humour comprehension also appear to be crucial for the comprehension of irony and sarcasm (in particular the IFG and mPFC). This is perhaps not surprising given the underlying processes involved in both (i.e., detection and resolution of incongruity, and the involvement of mentalising processes, see Obert et al., 2016, for further discussion).

The second brain network outlined by Vrticka et al. (2013) relates more to the emotional component of humour comprehension, and is described as recruiting the insula, the ventral anterior cingulate cortex (ACC), the supplementary motor area (SMA), and mesocorticolimbic dopaminergic brain areas. They also note that humour comprehension is often associated with activation in the amygdala (in relation to it being a 'relevance detector' since the signal has high social significance). Some previous studies investigating sarcasm, specifically, also report activation in the amygdala (e.g., Akimoto et al., 2014; Uchiyama et al., 2012). In the current study, we did not find activation in the amygdala for sarcastic materials. One possible reason for this might be that our control condition, literal praise, may also carry high social significance. Interestingly, Vrticka et al. (2013) note that most studies of humour lack conditions in which the control condition is a positive state without humour. The current control condition (literal praise) would arguably count as a positive state without humour, suggesting that further research is needed to examine amygdala involvement in humour. We did, however, find activation in other areas purported to be involved in the emotional component of humour comprehension, such as BA8 (which is part of the supplementary motor area), and BA46, which is part of the dlPFC (see also Akimoto et al., 2014 for discussion of this area in relation to

humour).

In sum, it would appear that in relation to literal controls, many more brain regions are activated for sarcastic than non-sarcastic irony. In particular, there is greater activation in parts of the IFG and more regions involved in humour comprehension, highlighting the importance of contrast detection and the elicitation of humour in sarcastic comments (discussed in more detail in section 3.3 below). In addition, there is activation in more areas of the mentalising network, supporting the notion that more complex mentalising operations are involved in the comprehension of sarcastic versus non-sarcastic irony. Finally, activation in both the left and right hemispheres contributed to the comprehension of sarcastic and non-sarcastic irony, adding support to the conclusion of Rapp et al. (2012) that the right hemisphere does not appear to have an outstanding role in figurative language processing.

3.3 (Sarcastic Irony - Literal) > (Non-sarcastic Irony - Literal), i.e., Sarcastic Irony > Non-sarcastic Irony

In the Sarcastic Irony > Non-sarcastic Irony contrast, the principal area with more activation was BA6 (right), which is part of the supplementary motor cortex. An account of the role of the SMA in language comprehension and production is presented in a recent review article by Hertrich, Dietrich, and Ackerman (2016). Hertrich et al. argue that the SMA plays a fundamental role in speech and language processing, particularly in cases where task demands are increased. In terms of connectivity, Hertrich et al. note that the SMA/pre-SMA receive subcortical input from structures such as the cerebellum and putamen (which are also active here). The major output pathways (from pre-SMA) are cortico-cortical associations with regions such as the prefrontal cortex and IFG (again, also active here). Thus, according to the

model of Hertrich et al., these structures function as a key interface between subcortical and cortical structures. As part of this network, the SMA (in particular, the pre-SMA) are involved not only in motor control during speech, but also in a number of other higher-order cognitive functions that are relevant to the current research, such as context integration, ambiguity resolution, and inhibition of incorrect representations. It is possible that sarcastic irony requires, for example, more contextual integration effort than non-sarcastic irony, given that speaker intent is an additional factor to be integrated in this case. Clearly, the role of the SMA in higher-order language comprehension requires further investigation.

Interestingly, the supplementary motor cortex has been identified as one of the key areas involved in the perception of humour (see Wild, Rodden, Grodd, & Ruch, 2003, for a review). In particular, it has been implicated in the emotional aspect of humour comprehension (see Vrticka et al., 2013, for a more recent overview). Interestingly, it has been shown to be activated during humour-induced smiling or laughter (Iwase et al., 2002). Given the fundamental role of laughter in mitigating negative emotional experiences (see Scott, Lavan, Chen, & McGettigan, 2014, for discussion), it is possible that smiling or laughter may be enhanced for sarcastic compared to non-sarcastic irony, due to the personal nature of the criticism in sarcastic cases.

In further relation to humour comprehension, we also see activation of subcortical structures such as the putamen. Although these regions did not form part of the current predictions, it is interesting to note that some subcortical areas have been implicated in the processing of humour in relation to irony (see Obert et al., 2016, for discussion), or as being activated during humour-induced smiling or laughter (Iwase et al., 2002). Other recent language studies (e.g., Viñas-Guash & Wu,

2017) highlight the potential role of this region in language comprehension more generally, arguing that contemporary neuroimaging techniques are revealing a language network which includes such brain structures that were not traditionally thought of as being involved in language comprehension. Viñas-Guash and Wu (2017) note that although a lot of recent research has pointed to a role for the putamen in language, its specific contribution is not yet clear (however, the left putamen may be involved in semantic processing).

Finally, we found the cerebellum, another subcortical structure, to be more activated in the sarcastic condition. The cerebellum has traditionally been associated with lower-level processes, such as motor functions (see e.g., Manto et al., 2012). However, recent research increasingly suggests a key role for the cerebellum in higher-level cognitive functions such as working memory (e.g., Thürling et al., 2012), and importantly, language (see Mariën et al. 2014, for a recent overview). Most relevant to the current experiment, the cerebellum has been implicated in the processing of figurative language, with evidence from both patients with cerebellar lesions (e.g., Cook, Murdoch, Cahill, & Whelan, 2004), and from recent neuroimaging studies (e.g., Benedek et al., 2014; Bosco et al., 2017; Rapp et al., 2012).

The key point for consideration here is why this region would be more active for sarcastic than non-sarcastic irony. One possibility is that sarcasm places increased cognitive demands on the reader (see Mariën et al., 2014). Another possibility is that it relates to the purported role of the cerebellum in the production of inner speech (e.g., Strick, Dum, & Fiez, 2009). Sarcastic irony is often associated with a certain tone of voice, and recent research indicates that readers will simulate implicit prosody in a silent reading task (see Yao & Scheepers, 2015, for a recent review, see also

Hertrich et al., 2016, discussed above, for related involvement of the SMA in inner speech processes). This process in relation to sarcasm comprehension is an interesting avenue for future research (see Matsui et al., 2016).

3.4 Limitations

There are a number of limitations to the current study. Firstly, since the major strength of fMRI is excellent spatial resolution, rather than excellent temporal resolution, the results of the current study are less informative regarding the time course of processes involved in the comprehension of irony. However, the main aim of the current study was to investigate the neural mechanisms underlying the comprehension of sarcastic versus non-sarcastic irony, as opposed to investigating questions relating to the timing of different processes (for recent work in this area using methodologies with excellent temporal resolution such as eye-tracking and event-related brain potentials see e.g., Au-Yeung, Kaakinen, Liversedge, & Benson, 2015; Filik et al., 2014; Filik & Moxey, 2010; Kaakinen, Olkonieni, Kinnari, & Hyönä, 2014; Olkonieni, Ranta, & Kaakinen, 2016; Regel, Coulson, & Gunter, 2010; Regel, Gunter, & Friederici, 2011; Regel, Meyer, & Gunter, 2014; Spotorno, Cheylus, Van Der Henst, & Noveck, 2013; Turcan & Filik, 2016).

Secondly, it is important to note that our materials were in the third-person, that is, critical comments were directed at a character in the scenario, rather than at the participants themselves. It is of course possible that comments would be processed differently if the criticism was directed at the participant rather than at someone else. However, we did attempt to mitigate this issue by assessing participants' ability to take another's perspective, and by including this in the analysis. Nevertheless, an interesting avenue for future studies would be to compare processing for comments

that are directed at the participants themselves as compared to those that are directed at another person (see e.g., Akimoto et al. 2014 for findings relating to first-person directed stimuli).

3.5 Conclusions

In conclusion, in the current study, we aimed to investigate the neural mechanisms underlying the comprehension of sarcastic versus non-sarcastic irony. Results showed that areas of the mPFC and IFG were more activated for non-sarcastic irony compared to literal controls, suggesting that readers do need to understand that the speaker's beliefs do not match what they are saying, and that some extra effort is involved in representing the literal and ironic state of affairs. Sarcastic irony showed more widespread activation in these areas, in particular in the IFG. In addition, sarcastic irony recruits areas which are involved in the emotional aspect of humour comprehension, as well as a number of subcortical structures. This would suggest that more complex operations are required for the comprehension of sarcastic than non-sarcastic irony, and supports the proposal that sarcasm may serve a number of social functions, such as allowing the speaker to be critical with the use of humour.

4. Footnotes

1. Participants also completed the SPR-III Psychopathy scale, but ultimately we did not have a large enough sample size to carry out meaningful correlations with this data.

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