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Research Report

Neural substrates of sarcasm: A functional magnetic-resonance imaging study

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ABSTRACT

The understanding of sarcasm reflects a complex process, which involves recognizing the beliefs of the speaker. There is a clear association between deficits in mentalizing, which is the ability to understand other people's behavior in terms of their mental state, and the understanding of sarcasm in individuals with autistic spectrum disorders. This suggests that mentalizing is important in pragmatic non-literal language comprehension. To highlight the neural substrates of sarcasm, 20 normal adult volunteers underwent functional magnetic-resonance imaging. We used scenario-reading tasks, in which sentences describing a certain situation were presented, followed by the protagonist's comments regarding that situation. Depending on the situation, the semantic content of the comments was classified as sarcastic, non-sarcastic, or contextually unconnected. As the combination of the first and second sentences represented discourse-level information that was not encoded in the individual sentences, sarcasm detection was represented as the differential activation induced by the second sentences. Sarcasm detection activated the left temporal pole, the superior temporal sulcus, the medial prefrontal cortex, and the inferior frontal gyrus (Brodmann's area [BA] 47). The left BA 47 was activated more prominently by sarcasm detection than by the first sentence. These findings indicate that the detection of sarcasm recruits the medial prefrontal cortex, which is part of the mentalizing system, as well as the neural substrates involved in reading sentences. The left BA 47 might therefore be where mentalizing and language processes interact during sarcasm detection.

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Abbreviations:
3D, three-dimensional
ANOVA, analysis of variance
AS, Asperger's syndrome
BA, Brodmann's area
EPI, echo-planar imaging
FA, flip angle
fMRI, functional magnetic-resonance imaging
FOV, field of view
GFi, inferior frontal gyrus
MNI, Montreal Neurological Institute
MPFC, medial prefrontal cortex
MP-RAGE, magnetization-prepared rapid-acquisition gradient-echo
NS, non-sarcasm condition
preSMA, pre-supplementary motor area
S, sarcasm condition
SD, standard deviation
SPM{*t*}, statistical parametric map of the *t*-statistic
STS, superior temporal sulcus
TE, echo time
TR, time interval between two successive acquisitions of the same image
U, unconnected condition
VOI, volume of interest

1. Introduction

The understanding of an utterance cannot be based solely on the meanings of the individual words (semantics) or the grammar by which they are connected (syntax); it also requires the correct perception of the meaning of the speaker in a social context (pragmatics). Irony is one form of pragmatics that is used to convey feelings in an indirect way (Shamay-Tsoory et al., 2005). Irony is characterized by opposition between the literal meaning of the sentence and the speaker's meaning (Haverkate, 1990; Winner, 1988). Sarcasm is a form of irony that is used in a hurtful or critical way (McDonald and Pearce, 1996). Sarcasm is usually used to communicate implicit criticism about the listener or the situation on occasions provoking a negative effect and is accompanied by disapproval, contempt, and scorn (Sperber and Wilson, 1986). Sarcasm can increase the perceived politeness of the criticism (Brown and Levinson, 1978), decrease the perceived threat and aggressiveness of the criticism (Dews and Winner, 1995), or create a humorous atmosphere (Dews and Winner, 1995).

Previous psycholinguistic models of sarcasm have focused on the process by which the intended meaning is communicated. According to Grice (1975), conversational inferences are made possible by implicit agreements between speakers and listeners. By cooperating with each other in communication, they observe certain conventions (maxims) in speech regarding the requirement, clarity, truthfulness, and relevance. An evident disregard of a conversational maxim can cause a listener to reinterpret the utterance in order to make sense of why it was said in such a manner. By transgressing conversational maxims, speakers can thus communicate indirectly (Brown and Levinson, 1978).

The traditional model fails to account for the integral role that the speaker's attitude plays in a sarcastic retort (McDonald and Pearce, 1996). Focusing on the speaker's attitude, Sperber and Wilson (1986, 1987) postulated an alternative theory of irony in terms of the role of relevance in communication. They argued that every utterance has a single interpretation, which is a product of the listener's search for the relevance that the utterance has to its context. Sarcastic comments are recognized as relevant because they remind the listener of a proposition that had been asserted at an earlier time or some other shared knowledge that has since proven to be wrong. Thus, the sarcastic statement is meant literally as an 'echo' of a proposition that has been previously stated. Speakers echo the earlier proposition; however, by doing so, they also impart their negative attitude towards it. This echoic model places attitude as central to sarcasm, emphasizes the literal meaning as the only meaning conveyed, and argues that a sarcastic interpretation is derived by recognizing the relevance of the literal meaning (McDonald and Pearce, 1996).

Both models suggest that understanding sarcastic utterances depends on the ability to understand the social cues (such as intentions, beliefs, and emotions) expressed in the situation—that is, the social cognition (Shamay-Tsoory et al., 2005). The traditional model stresses the contradictory nature of the sarcastic remark as the cue of the speaker's intention, whereas the echoic model extends it to the relevance of the sarcastic utterance in a broader context.

A key aspect of social cognition is the ability to infer other people's mental state, thoughts, and feelings, which is commonly referred to as mentalizing (Frith and Frith, 2003). In predicting other individuals' behavior through mentalizing, it is implicitly assumed that the behavior of others is determined by their desires, attitudes, and beliefs. These are not states of the world, but rather states of the mind. This is important because, in everyday life, beliefs rather than reality determine how people behave (Frith and Frith, 2003). A typical example of false-belief task is like this: Maxi has some chocolate and puts it into a blue cupboard. Maxi goes out. Now his mother comes in and moves the chocolate to a green cupboard. Maxi comes back to get his chocolate. Where will Maxi look for the chocolate? The answer is: Maxi will look in the blue cupboard because this is where he falsely believes the chocolate to be (Wimmer and Perner, 1983).

Recent findings in developmental and neuropsychological research suggest that understanding irony involves interpreting social cues and also requires mentalizing (Frith and Frith, 2003). The difficulties that small children might have in understanding irony are related to their problems with inferring the speaker's beliefs and intentions (Sullivan et al., 1995; Winner and Leekam, 1991). Understanding irony requires first-order intentionality about the speaker's beliefs (to avoid interpreting irony as a mistake), as well as second-order intentionality about the speaker's beliefs regarding the listener's beliefs (to avoid interpreting irony as a lie; Dews and Winner, 1997). There is also good empirical evidence for a clear association between deficits in mentalizing and pragmatic understanding in individuals with autism. The inability to report thoughts about thoughts (that is, second-order meta-representations) is thought to explain why autistic individuals, especially those with Asperger's syndrome (AS), exhibit communication problems (Adachi et al., 2004; Frith and Happé, 1994; Happé, 1994; Leekam and Prior, 1994).

The same pattern of impairment has been reported in lesion studies (Dennis et al., 2001). Winner et al. (1998) have suggested that individuals with right hemisphere damage are unable to distinguish lies from jokes and that this inability is related to a difficulty in attributing second-order mental states (Winner et al., 1998). Prefrontal brain damage was shown to be associated with both impaired empathic ability and impaired ability to interpret ironic utterances (Shamay et al., 2002; Shamay-Tsoory et al., 2005).

Previous neuroimaging studies on the neural substrates of mentalizing have reported the involvement of the medial prefrontal cortex (MPFC), including the anterior cingulate cortex, posterior superior temporal sulcus (STS), temporal pole, and amygdala (Frith and Frith, 2003; Gallagher and Frith, 2003; Siegal and Varley, 2002). Most neuroimaging studies of mentalizing are based on the theory of mind with the false-belief task. In this approach, a volunteer is scanned while reading a series of short stories in which the behavior of the protagonist is determined by his or her false belief about the situation. Stories matched for difficulty are utilized as controls. These stories also involve people, but the critical events are explained in terms of physical causality (Frith and Frith, 2003).

Although the topic of pragmatic language and its relation to mentalizing is receiving increasing interest (Frith and Frith, 2003), little is known about the neural correlates of sarcasm. As the models of the sarcasm suggest, lexico-semantic and mentalizing processes are thought to be closely interrelated. However, to the best of our knowledge, only one pediatric functional magnetic-resonance imaging (fMRI) study (Wang et al., 2006) has previously investigated the neural substrates of sarcasm. The purpose of the present study was to identify the neural substrates of sarcasm detection using fMRI. Our hypothesis was that sarcasm comprehension provokes linguistic, mentalizing, and emotional processes (Shamay-Tsoory et al., 2005) and hence activates the corresponding neural substrates which may be partly overlapped. The following example sentences are representative of those that were visually presented in the non-sarcasm condition in the present study.

(S1) When Takuya's mother came home, his clothes were strewn all over his room. When she saw this, she said to him: (S2) why do you always leave your room so messy? (non-sarcastic). Here, the listener (Takuya) understands that S2 is an overt expression of the speaker's (his mother's) thoughts evoked by S1 and hence is relevant to the context.

(S1) When Takuya's mother came home, his clothes were strewn all over his room. When she saw this, she said to him: (S2) how do you always keep your room so tidy? (sarcastic). Here, the listener understands that S2 is a clue to the thoughts of the speaker as it is an interpretation of a further thought evoked by S1. When Takuya's mother says "how do you always keep your room so tidy?" she is commenting on her prior belief that Takuya should keep his room tidy (echo). The mother is essentially alluding to this prior belief and is thus conveying her negative attitude towards an attributed thought (that is, that Takuya leaves his room in a mess).

Hence, the processing of sarcasm requires meta-representational reasoning (Gibbs, 1999; Happé, 1993); sarcastic sentences are processed interpretively because they require the recognition of thoughts about attributed thoughts (that is, second-order meta-representations) to understand what the speaker is implying by sarcastic statements. Thus, we hypothesize that the neural activation evoked by S2 is related to the mentalizing process (Frith and Frith, 2003), in addition to the lexico-semantic processes. Furthermore, as S2 in the latter example conveyed the mothers affect (anger or disappointment), the neural substrates of the affecting process would also be activated.

2. Results

2.1. *Task performance*

The mean (±standard deviation [SD]) percentage of correct answers was 96.8±5.48% for the sarcastic condition, 94.8±4.66% for the non-sarcastic condition, and 98.8±3.31% for the unconnected condition. Although the performance for the unconnected condition was slightly better than those for the other conditions ($P<0.05$, one-way repeated measure analysis of variance [ANOVA]), the participants performed all conditions satisfactorily.

Table 1 – Brain regions active during reading S1

P	Z-value	MNI coordinate {mm} x	y	z	Side	Location	BA
<0.001	5.96	−2	2	70	L	PreSMA	6
0.028	5.1	8	16	46	R	PreSMA	6
0.023	5.15	−6	18	38	L	Anterior GC	32
0.003	5.54	2	−36	28	R	Posterior GC	31
0.003	5.58	−46	0	48	L	PMd	6
0.012	5.3	34	8	58	R	PMd	6
0.004	5.52	−60	−12	40	L	PMv	6
0.01	5.33	−58	−14	14	L	GPrC	6
0.001	5.68	−46	−18	44	L	SM1	4/3
0.001	5.68	46	40	32	R	GFm	9
0.021	5.17	38	48	22	R	GFm	10
0.002	5.61	−34	30	−24	L	GFi	47
0.007	5.41	26	36	−20	R	GFi	47
0.027	5.11	−42	6	30	L	GFi	44
0.013	5.29	−56	28	14	L	GFi	45
0.001	5.83	−58	0	−16	L	GTm	21
0.029	5.09	−54	−8	−20	L	GTi	20
0.01	5.34	−54	−38	0	L	GTm	21
0.001	5.76	58	12	−14	R	GTs	38
0.007	5.41	−16	−74	24	L	GOm	19
<0.001	6.87	−38	−84	−6	L	GOi	18
<0.001	7.05	28	−98	−12	R	GOi	18
<0.001	6.54	40	−82	−4	R	GOi	19
<0.001	Inf	−14	−94	−12	L	GL	17
<0.001	6.9	10	−94	−4	R	GL	17
<0.001	7.15	−40	−66	−30	L	Cerebellum	
<0.001	6.7	36	−70	−26	R	Cerebellum	
<0.001	6.56	0	−54	−38		Cerebellar vermis	
<0.001	6.89	−10	−28	−6	L	Midbrain	
<0.001	6.69	22	−28	−2	R	Midbrain	
0.015	5.25	−22	−6	−2	L	Globus pallidus	
0.011	5.33	20	−10	−2	R	Globus pallidus	
0.004	5.52	12	−6	10	R	Thalamus	
0.005	5.47	−10	−16	8	L	Thalamus	
0.005	5.47	26	−2	−18	R	Amygdala	
0.003	5.54	−34	−10	−20	L	Hi	

Abbreviations: BA, Brodmann's area; GC, cingulate gyrus; GFi, inferior frontal gyrus; GFm, middle frontal gyrus; GFs, superior frontal gyrus; GL, lingual gyrus; GOi, inferior occipital gyrus; GPrC, precentral gyrus; GTi, inferior temporal gyrus; GTm, middle temporal gyrus; GTs, superior temporal gyrus; Hi, hippocampus; PMd, dorsal premotor cortex; PMv, ventral premotor cortex: preSMA, pre-supplementary motor area; SM1, primary sensorimotor cortex. L, left; R, right. All P values are corrected for multiple comparisons at voxel level.

2.2. *Group analysis with a random-effect model*

Reading the first sentence (S1) compared with the baseline condition with fixation cross produced bilateral activation of the following: the pre-supplementary motor area (preSMA), anterior and posterior cingulate cortex, dorsal premotor cortex, inferior frontal gyrus (GFi), Brodmann's area (BA) 47, occipital cortex, cerebellum, thalamus, midbrain, and globus pallidus; the left ventral premotor cortex, primary somatosensory cortex, GFi (BA 44 and BA 45), middle and inferior temporal gyri, and hippocampus; and the right amygdala and middle frontal gyrus (Table 1 and Fig. 1).

Contrasting the sarcasm (S)/non-sarcasm (NS) conditions with the unconnected (UC) condition revealed that sarcasm detection activated the left GFi (BA 47), temporal pole, STS (BA 21/22) and MPFC, preSMA, and cerebellum bilaterally (Table 2 and Fig. 2). S/NS contrasted with UC should represent sarcasm detection because during S/NS the process of sarcasm discrimination will be held even if the stimuli are actually non-sarcastic. There was no significant activation by the contrast of S–NS.

Within these sarcasm detection-related areas, the relationship between S1- and S2-related activation was investigated to determine whether sarcasm detection was related to the lexico-semantic processes. Volume-of-interest (VOI) analyses in four regions (MPFC, IFG, STS, and temporal pole) were performed based on a 5-mm diameter spherical volume centered on the coordinates of maximum activation in the sarcasm-detection condition (S+NS–2UC). S1 activated the preSMA (BA 6; Montreal Neurological Institute (MNI) coordinates, $x=-6$, $y=16$, $z=58$; Evans et al., 1994) and the MPFC (BA 9; $x=-8$, $y=60$, $z=28$; Fig. 2). By contrast, another activation cluster located in BA 8 ($x=-6$, $y=44$, $z=42$) did not show significant activation by S1. The activation of BA 47 was more prominent for S2 than for S1 ($F(2.076,39.44)=23.96$, $P<0.05$; $P=0.010$, *post hoc* comparison with Bonferroni correction).

3. Discussion

3.1. *Brain regions active during sarcasm detection*

During S2, the sarcasm-detection tasks (S/NS) contrasted with the UC produced co-activation of the MPFC, preSMA, temporal pole, STS, and GFi. Co-activation of the temporal pole, STS, and MPFC has been observed during mentalizing using written stories or other episodic stimuli (Fletcher et al., 1995; Gallagher et al., 2000; Vogeley et al., 2001) and with cartoons (Brunet et al., 2000; Gallagher et al., 2000). These areas were also activated by inferring the knowledge and beliefs of someone who lived a long time ago (such as Christopher Columbus; Goel et al., 1995) or by social norm transgression (Berthoz et al., 2002). In addition to these explicit mentalizing tasks, implicit mentalizing tasks – such as the attribution of intention and desires to moving triangles – also activated these brain areas (Castelli et al., 2000).

3.1.1. *Temporal regions*

The temporal pole is a potential site for the convergence of all sensory modalities, as well as limbic inputs (Moran et al., 1987). The left temporal pole is frequently activated in studies of language and semantics (Bottini et al., 1994; Fletcher et al., 1995; Maguire et al., 1999; Vandenberghe et al., 1996, 2002). It is involved in the construction of sentence meaning from a syntactic combination of meaningful words (Vandenberghe et al., 2002).

In addition, the left temporal pole is activated during memory retrieval, particularly during autobiographical memory retrieval (Fink et al., 1996; Maguire and Mummery, 1999; Maguire et al., 2000). Based on these findings, Frith and Frith (2003) speculated that the left temporal pole is concerned with generating, on the basis of past experience, a wider

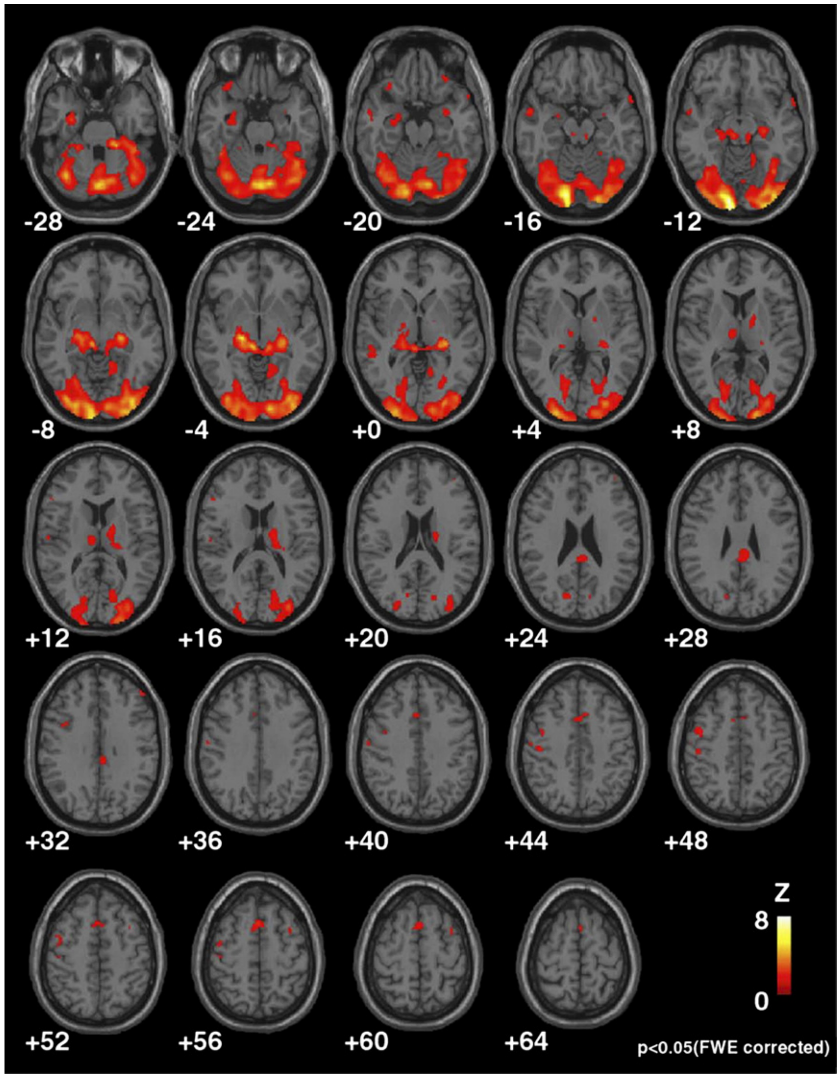

Fig. 1 – Brain regions that were active while reading the first sentence compared with the baseline. Activated foci are shown as pseudocolor fMRI scans superimposed on a high-resolution anatomical MRI in 24 contiguous transaxial planes with a 4-mm interval, extending from the MNI coordinates $z = -28$ (top left) to $z = +64$ (bottom right). The statistical threshold was set at $P < 0.05$, with a family-wise error corrected for multiple comparisons at the voxel level.

semantic and emotional context or script (Schank and Abelson, 1977) for the material currently being processed. Scripts are built up through experience and record the particular goals and activities that take place in a specific setting at a certain time. Identifying which script is most appropriate to a given situation is of considerable help in predicting what people are going to do; hence, it aids the interpretation of stories and pictures. Scripts provide a useful framework within which mentalizing can be applied because events rarely conform exactly to the established script, and mentalizing is needed to understand the deviations (Frith and Frith, 2003). In this context, the activation of the left temporal lobe by S2 is related to script retrieval, which is a prerequisite for the detection of sarcasm as it represents a deviation from the script.

The left middle temporal gyrus/STS area is engaged in semantic integration at the sentence level (Noppeney et al., 2005; Vandenberghe et al., 2002). Noppeney et al. (2005) reported that increased activation of the left STS region is associated with high reading ability.

In the present study, the temporal areas were activated by both S1 and S2. Considering that the left temporal structures are thought to form part of the sentence-comprehension system (Noppeney et al., 2005), the activation in this region might not be related specifically to the detection of sarcasm.

3.1.2. MPFC

The present study showed that sarcasm detection activated the MPFC (BA 8 and BA 9) and preSMA. The MPFC was activated only during the S/NS conditions, with no significant activation during the UC condition. By contrast, the preSMA was activated by both S1 and S2 (Fig. 1). Hence, the preSMA might be related to non-specific language processing, such as articulatory rehearsal (Paulesu et al., 1993). Part of the MPFC (BA 8; $x = -6$, $y = 44$, $z = 42$) was not activated by S1 and hence

Table 2 – Brain regions active during sarcasm detection

P	Z-value	MNI coordinate {mm}			Side	Location	BA
		x	y	z			
<0.001	6	−6	16	58	L	PreSMA	6
0.014	5.25	−6	44	42	L	GFd	8
0.003	5.56	−8	60	28	L	GFd	9
0.006	5.44	−60	22	12	L	GFi	45
0.005	5.45	−56	24	−6	L	GFi	47
0.045	4.96	−46	18	−10	L	GFi	47
<0.001	5.96	−52	8	−30	L	GTm	21
0.004	5.48	−56	−10	−12	L	STS	21/22
0.008	5.37	−56	−28	−2	L	STS	21/22
0.001	5.77	28	−82	−34	R	Cerebellum	

Abbreviations: BA, Brodmann's area; GFd, medial frontal gyrus; GFi, inferior frontal gyrus; GTm, middle temporal gyrus; GTs, superior temporal gyrus; STS, superior temporal sulcus. L, left; R, right. All P values are corrected for multiple comparisons at voxel level.

might not be directly related to lexical processing; instead, this region seemed to be linked specifically to the non-literal or pragmatic component of sarcasm detection.

The MPFC has direct connections to the temporal pole and the STS (Bachevalier et al., 1997) and is related to the performance of tasks involving the theory of mind (Frith and Frith, 2003), thus comprising part of the 'social brain' (Brothers, 1990). Frith and Frith (2003) suggested that MPFC activity reflects how a person interprets and utilizes the signals that elicit mentalizing. In addition to the mentalizing task, the MPFC is activated by inductive reasoning compared with deductive reasoning (Goel et al., 1997). Valid deductive arguments include the claim that their premises provide absolute grounds for accepting the conclusion. By contrast, in inductive arguments, the premises provide only limited grounds for accepting the conclusion. Hence, induction is typically viewed as a form of hypothesis generation and testing, where the crucial issue is one of searching a large database and determining which pieces of information are relevant and how they are to be mapped onto the present situation. Based on this finding, Goel et al. (1997) suggested that the MPFC activation might be associated with inductive reasoning involving generalization and abstraction over world knowledge rather than mental state terms. In line with this view, the MPFC was activated by tasks other than mentalizing, such as linguistic coherence judgment (Ferstl and von Cramon, 2002), evaluative judgment (Zysset et al., 2002), self-

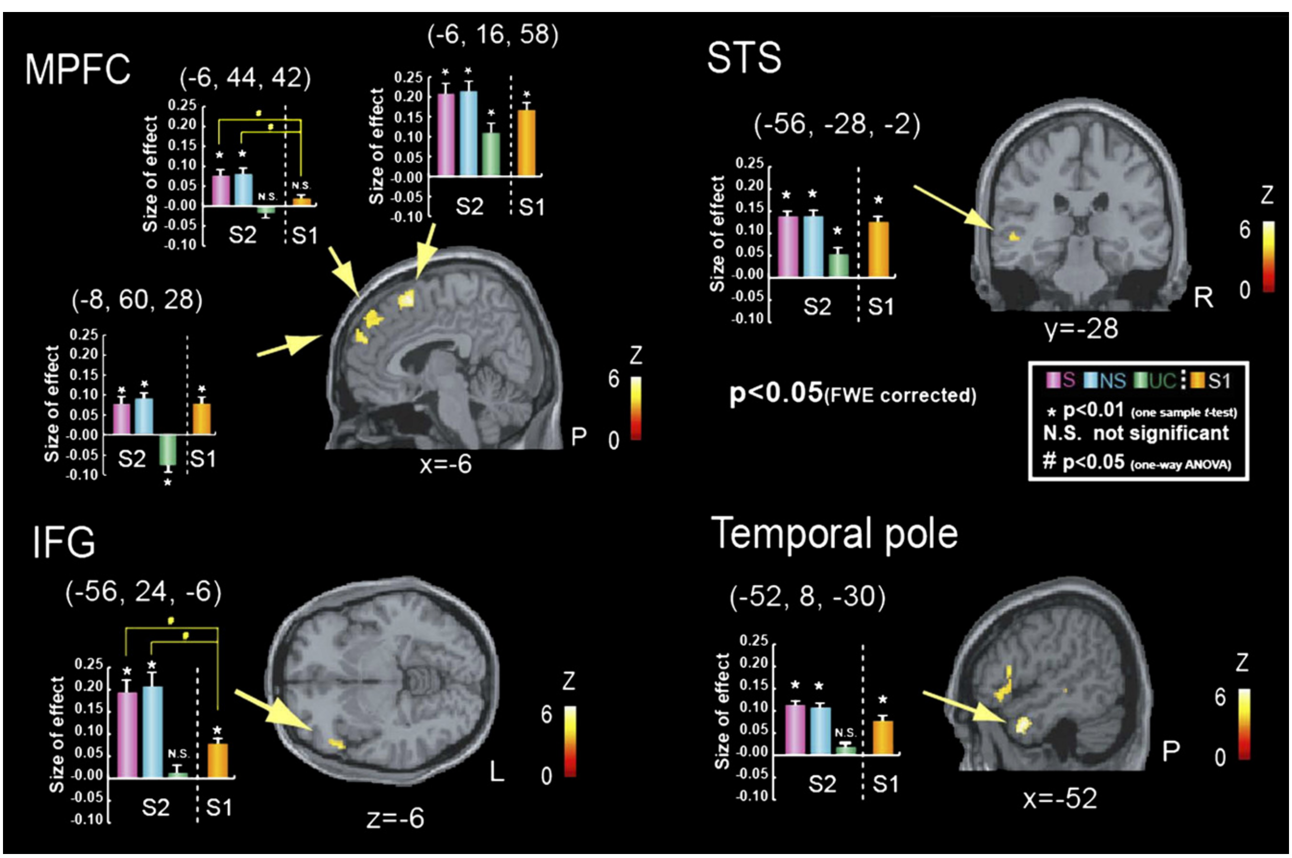

Fig. 2 – Group analysis of sarcasm detection (S+NS–2UC). The significantly activated areas are superimposed on T1-weighted high-resolution MRI of a single subject who was unrelated to this study. The statistical threshold was set at *P*<0.05 corrected for multiple comparisons at the voxel level. L, left; P, posterior; R, right. Task-related signal change in each condition in the MPFC, left GFi, left STS, and left temporal pole is also shown with their MNI coordinates. The sizes of the effects during the S (pink), NS (blue), UC (green), and S1 (orange) conditions are presented as the mean of 20 participants. Error bars indicate the standard error of the mean.

referential judgment (Gusnard et al., 2001), moral judgment (Greene et al., 2001), pragmatic comprehension (Bottini et al., 1994; Nichelli et al., 1995), and story comprehension (Maguire et al., 1999). Ferstl and von Cramon (2002) argued that the MPFC is probably related to tasks requiring self-guided non-automatic cognitive processes, such as mentalizing and coherence tasks. To summarize, the MPFC region that was activated specifically by the sarcasm-detection task was probably related to the mentalizing process as a type of inductive reasoning; that is, recognition of the attitude of the ironic protagonist (second-order representation) that was pragmatically relevant to the context given by S1.

3.1.3. *Inferior prefrontal cortex*

The left IFG showed activation during the presentation of S1 and was more prominently activated during the sarcasm-detection tasks (S/NS). The ventral portion of the inferior prefrontal cortex (mainly BA 47) is specifically involved in semantic processing during the comprehension of sentences (Dapretto and Bookheimer, 1999) and metaphors (Rapp et al., 2004). BA 47 might serve as a semantic executive system (Gabrieli et al., 1996; Kapur et al., 1994; Wagner et al., 1997), which is engaged by three processes: semantic retrieval, selection, and evaluation. In the S and NS conditions, the semantic processing of S2 was evaluated in the context provided by primary pragmatic knowledge (such as social norms) and the secondary pragmatic knowledge given by S1. By contrast, in the UC condition, the semantic processing during S2 was not related to the context of the previous sentence. Hence, the more prominent activation during S/NS presentation compared with that seen in the UC condition might represent the context-dependent evaluation or interpretation of S2. In fact, S/NS consisted of single short sentence while S1 comprised multiple longer sentences. This was because S1 was the scenario explaining the situation, whereas the S/NS was a brief comment on the situation. Despite this difference in the stimuli, BA 47 was more prominently activated by S/NS than by S1. These findings suggest that BA 47 is the site of the integration of semantic and mentalizing processes that occurs during sarcasm detection.

Another interpretation of the activation in the left IFG is related to the evoked negative affect. Sarcasm is generally used on occasions that provoke a negative affect and is often accompanied by disapproval, contempt, and scorn (Sperber and Wilson, 1986). Hence, sarcasm-related activation might be associated with the negative affect. A previous neuroimaging study reported that violation of social norms activated the BA 47 (Berthoz et al., 2002). Clinical observations in humans, and experimental reports in primates, have consistently indicated that the orbitofrontal cortex is engaged in the regulation of social and aggressive behavior (Blair and Cipolotti, 2000; Damasio et al., 1994; Davidson et al., 2000; Grafman et al., 1996; Pietrini et al., 2000; Rolls, 2000). The left orbitofrontal cortex (BA 10 and BA 47) was previously found to be activated by angry expressions (Kesler-West et al., 2001; Sprengelmeyer et al., 1998). This region is also activated under conditions when an individual is induced to feel angry (Dougherty et al., 1999). Thus, this region of the BA 47 responds not only to the angry expressions of others, but also to stimuli detailing actions that are likely to cause others to become angry (Berthoz et al., 2002), such as sarcasm. In the present study, however, the effect of sarcasm such as raised anger evoked by the sarcastic expression was not apparent by the contrast of S–NS condition. Further study is necessary to confirm the emotional response to the sarcasm.

3.1.4. *Non-verbal cues in sarcastic expression*

Neither traditional (Grice, 1975) nor echoic (Sperber and Wilson, 1986) models address the role of non-verbal information, such as prosody, which is important in detecting a speaker's negative attitude (Utsumi, 2000). By extending the two models, Utsumi (2000) proposed that verbal irony is a verbal expression (utterance or statement) that implicitly displays an ironic environment that consists of the speaker's expectation, an incongruity between the expectation and the reality, and the speaker's negative attitude towards this incongruity. This implicit display is typically achieved by an utterance that alludes to the speaker's expectation, violates one of the pragmatic principles, and is accompanied by indirect cues. Ironic cues are used for indirectly expressing speakers' negative attitudes. These cues include hyperbolic words/phrases and intensives, interjections, prosodic features (such as intonation, tone of voice, exaggerated stress, and nasalization), and non-verbal cues (such as facial expressions and behavioral cues; Utsumi, 2000). The degree of ironicalness is quantitatively defined as a measure of similarity between the prototype of irony and an utterance; hence, the ironical character of an utterance is a matter of degree. Therefore, prosodic cues enhance the ironicalness by indirectly expressing speakers' negative attitudes. The present study adopted reading materials; hence, the effect of prosodic features or nonverbal cues could not be evaluated. The effect of the indirect cues is to be explored in future study.

4. Conclusions

In conclusion, sarcasm detection activated the neural circuits involved in mentalizing processes, as well as those of the semantic executive system. This is consistent with the notion that pragmatic processes, such as sarcasm, are closely related to mentalizing functions (Frith and Frith, 2003). We suggest that the left BA 47 might be where mentalizing and language processes interact during sarcasm detection.

5. Experimental procedures

5.1. *Participants*

Undergraduate and graduate students from local universities were recruited as paid volunteers. In total, 20 right-handed healthy volunteers took part in the study: 10 females (mean age ± SD = 21.8 ± 3.0 years) and 10 males (mean age ± SD = 22.0 ± 2.4 years) with an overall mean age ± SD of 21.9 ± 2.7 years and an age range of 19–29 years. The mean number of years of education was 15.9 ± 2.7. We measured visual acuity before the experiment and confirmed that all participants were suitable, with or without correction, to participate in the experiment (that is, ≥1.0 decimal visual acuity). Handedness was determined using the Edinburgh Handedness Inventory (Oldfield, 1971). All participants were educated beyond college level. Past history was taken using a medical check list. No participant had a history of neurological or psychiatric disease, drug or alcohol abuse, or long-lasting unconsciousness or significant head injuries. Written informed consent to take part in the study was obtained following procedures approved by the Ethical Committee of the National Institute for Physiological Sciences, Japan.

5.2. *Tasks*

All participants completed the sarcastic-scenario task (Adachi et al., 2004). The scenarios consisted of two parts. The first part (S1) explained the situation of one protagonist, while the second part (S2) gave the comment of another protagonist. In the sarcastic scenario, the comment did not directly match the situation and implied the opposite feeling (such as blame or disappointment). In the non-sarcastic scenario, the comment matched the situation and hence reflected the protagonist's true feeling. In the UC, the comments were replaced by a sentence that was unrelated to the situation, indicating which button should be pressed. Representative example sentences are as follows. (S1) When Takuya's mother came home, his clothes were strewn all over his room. When she saw this, she said to him: sarcastic response (S2) "how do you always keep your room so tidy?"; non-sarcastic response (S2) "why do you always keep your room so messy?"; unconnected response (S2) "the button you should press is button no. 1." During S and NS conditions, the process of sarcasm comprehension is definitely necessary to determine which button should be pressed, whereas in UC condition this process is absent. Therefore, comparison between these conditions should depict the areas that include the neural representation of sarcasm comprehension.

5.2.1. *Presentation of the stimuli and behavioral responses*

All stimuli were prepared and presented using Presentation software (Neurobehavioral Systems, CA, USA) on a microcomputer (Dimension 8200, Dell Computer Co., Texas, USA). Using an LCD projector (DLA-M200L, Victor, Yokohama, Japan), the visual stimuli were projected onto a half-transparent viewing screen located behind the head coil, and the participants viewed the stimuli through a mirror. The sentence stimuli were written in Japanese and presented as white letters against a black background. The maximum visual angle was 20.8° (width) by 9.5° (height).

S1 was presented on the screen for 5 s followed by a cross-hair for 2 s. S2 then appeared for 1 s followed by the cross-hair for 2 s. Then, a question mark '?' was presented for 1 s. The participant was required to press, as quickly as possible, the button under the right middle finger if S2 was sarcastic, and under right index finger if S2 was non-sarcastic. When S2 indicated which button to press, the participant was required to press the button as indicated. The trial finished with the presentation of the fixation cross for 1 s. And hence subjects had 2 s to respond.

We used an event-related design to minimize habituation and learning effects. In addition to the task conditions, a baseline condition was included, during which only the fixation cross was presented. During each scanning session, 40 stimuli (10 sarcastic scenarios, 10 non-sarcastic scenarios, 10 unconnected conditions, and 10 baseline conditions) were presented. The distribution of the stimulus-onset asynchronies (SOAs) of each condition were optimized (Sadato et al., 2005; Saito et al., 2005). We wanted to maximize the efficiency with which we could detect differences between (S+NS)/2 and UC, S–NS, S, NS, and UC. To do this, the distributions of the SOAs for all conditions were determined as follows (Friston et al., 1999b). In one session, the order of 30 events (10 for each condition) was randomly permutated to generate a set of four vectors (1×30 matrix) indicating the presence (1) or absence (0) of a particular event and hence representing the distribution of the SOAs of each condition (SOA vectors). A design matrix **X** incorporating three conditions (S, NS, and UC) and the S1 presentation (fixed SOA) was created by convolving a set of four vectors with a hemodynamic response function (h) as follows:

$$X = [s1, s, ns, uc] \otimes h$$

Here, $s1$ corresponds to S1, s corresponds to S, ns corresponds to NS, and uc corresponds to UC. The efficiency of the estimations of S+NS–2UC, S–NS, S, NS, and UC was evaluated using the inverse of the covariance of the contrast of the parameter estimates (Friston et al., 1999b) as follows:

$$\mathrm{var}\{c^T\hat{\beta}\} = \sigma^2 c^T (X^T X)^{-1} c,$$
$$\mathrm{Efficiency} = \mathrm{trace}\,\{c^T (X^T X)^{-1} c\}^{-1}.$$

Here, $c=(0, 1, 1, -2)$ for S+NS–2UC, $(0, 1, -1, 0)$ for S–NS, $(0, 1, 0, 0)$ for S, $(0, 0, 1, 0)$ for NS, and $(0, 0, 0, 1)$ for UC. From the 100,000 randomly generated sets of SOA vectors, we selected the most efficient one, which showed a maximum of the sum of the squares of the efficiency vectors for five contrasts.

Each participant completed three sessions, the order of which was counterbalanced across subjects. This was to increase the repetition number for each condition, while keeping the duration of the session reasonably short. We prepared 60 scenario stimuli in total (20 sarcastic scenarios, 20 non-sarcastic scenarios, and 20 unconnected sentences); therefore, the same scenarios were repeated no more than twice. The participants underwent a training session prior to the fMRI experiment with the stimuli that were not used during the fMRI experiment.

5.3. *fMRI data acquisition*

In each session, a time course series of 196 volumes was acquired using T2*-weighted gradient-echo echo-planar imaging (EPI) sequences with a 3.0 T MR imager (Allegra, Siemens, Erlangen, Germany). Each volume consisted of 42 transaxial slices, with a thickness of 3.0 mm and a 0.3-mm gap between slices. These scans covered the entire cerebral and cerebellar cortices. Oblique scanning was used to exclude the eyeballs from the images. The time interval between two successive acquisitions of the same image (TR) was 2500 ms with a flip angle (FA) of 80° and a 30-ms echo time (TE). The field of view (FOV) was 192 mm, and the in-plane matrix size was 64×64 pixels. For anatomical reference, T1-weighted magnetization-prepared rapid-acquisition gradient-echo (MP-RAGE) images (TR=1500 ms, TE=4.38 ms, FA=8°) collected at the same positions as the echo-planar images and T1-weighted high-resolution three-dimensional (3D) MP-RAGE images covering the whole brain (TR = 2500 ms, TE = 4.38 ms, FA = 8°, FOV = 230 mm, and matrix size = 256 × 256 mm) were obtained for each participant.

5.4. *Data analysis*

The data were analyzed using statistical parametric mapping (SPM2; Wellcome Department of Cognitive Neurology, London, UK; Friston et al., 1995a, b) implemented in Matlab (Mathworks, Sherborn, MA, USA). The first four volumes of each fMRI session were discarded to allow for stabilization of the magnetization, and the remaining 192 volumes per session (a total of 576 volumes per participant) were used for analysis. After correcting for differences in slice timing within each image volume (Buchel and Friston, 1997), all volumes were realigned for motion correction. The first image produced by EPI, to which all others were realigned, was co-registered onto the canonical image. The parameters for affine and nonlinear transformation into a template of EPI volumes that was already fitted to a standard stereotaxic space (Evans et al., 1994) were estimated by the least-square means. The parameters were applied to the high-resolution 3D T1-weighted MR images. The anatomically normalized fMRI data were spatially smoothed using a Gaussian kernel of 8 mm (full width at half maximum) in the x, y, and z axes.

Statistical analysis was conducted at two levels. First, the individual task-related activation was evaluated (Friston et al., 1995b). Second, the summary data for each individual were analyzed using a random-effect model (Friston et al., 1999a) to make inferences at a population level.

5.4.1. *Individual analysis*

The signal intensity from the images was proportionally scaled by setting the whole-brain mean value to 100 arbitrary units. The signal time course for each participant was modeled with a general linear model. Regressors of interest (trial effects) were generated using a box-car function convolved with a hemodynamic-response function. Regressors that were of no interest, such as the session effect and high-pass filtering (61 s), were also included. Therefore, it is regarded as the mixed effect model, in which the fixed effects represent differences between the conditions (S, NS, UC) and the random effects represent differences between sessions. The explanatory variables were centered to zero. To test hypotheses about regionally specific effects, the estimates for each model parameter were compared with the linear contrasts. We set up the following two contrasts to identify the neural substrates relevant to sarcasm. First, we delineated the activated regions related to the S1 presentation. Second, the regions activated during both the S and NS conditions were compared with the UC condition (S + NS–2UC). Both the S and NS tasks required the participants to judge whether S2 indicated the protagonist's true feeling. During the UC, participants were only required to read a sentence and respond by pressing a button. Therefore, we defined this contrast (S + NS–2UC) as the sarcasm-detection contrast. The set of voxel values resulting from each comparison yielded a statistical parametric map of the t-statistic, SPM{t}. The SPM{t} was transformed to normal distribution units (SPM{Z}). The statistical threshold was set at $P < 0.05$ with a correction for multiple comparisons at the voxel level for the entire brain (Friston et al., 1996).

5.4.2. *Group analysis with the random-effect model*

The weighted sum of the parameter estimates in the individual analysis constituted 'contrast' images, which were used for the group analysis (Friston et al., 1999a). The contrast images obtained via the individual analysis represent the normalized task-related increment of the MR signal for each participant. For each contrast, an unpaired Student's t-test was performed for every voxel within the brain to obtain population inferences. The resulting set of voxel values for each contrast constituted a (SPM{t}). This was transformed to normal distribution units (SPM{Z}). The statistical threshold was set at $P < 0.05$ with a correction for multiple comparisons at the voxel level for the entire brain (Friston et al., 1996).

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