Irony Comprehension: Social Conceptual Knowledge and Emotional Response

Yoritaka Akimoto,^{1*} Motoaki Sugiura,^{1,2} Yukihiro Yomogida,^{3,4}
Carlos Makoto Miyauchi,¹ Shiho Miyazawa,⁵ and Ryuta Kawashima^{1,6,7}

¹Department of Functional Brain Imaging, Institute of Development, Aging and Cancer,
Tohoku University, Sendai, Japan

²International Research Institute of Disaster Science, Tohoku University, Sendai, Japan

³Brain Science Institute, Tamagawa University, Tokyo, Japan

⁴Japan Society for the Promotion of Science, Tokyo, Japan

⁵Department of Biological Psychiatry, Tohoku University Graduate School of Medicine, Sendai, Japan

⁶Division of Developmental Cognitive Neuroscience, Institute of Development, Aging and Cancer,
Tohoku University, Sendai, Japan

⁷Smart Ageing International Research Center, Institute of Development, Aging and Cancer,
Tohoku University, Sendai, Japan

Abstract: Verbal irony conveys various emotional messages, from criticism to humor, that differ from the meaning of the actual words. To understand irony, we need conceptual knowledge of irony in addition to an understanding of context. We investigated the neural mechanism of irony comprehension, focusing on two overlooked issues: conceptual knowledge and emotional response. We studied 35 healthy subjects who underwent functional MRI. During the scan, the subject examined first-person-view stories describing verbal interactions, some of which included irony directed toward the subject. After MRI, the subject viewed the stories again and rated the degree of irony, humor, and negative emotion evoked by the statements. We identified several key findings about irony comprehension: (1) the right anterior superior temporal gyrus may be responsible for representing social conceptual knowledge of irony, (2) activation in the medial prefrontal cortex and the right anterior inferior temporal gyrus might underlie the understanding of context, (3) modulation of activity in the right amygdala, hippocampus, and parahippocampal gyrus is associated with the degree of irony perceived, and (4) modulation of activity in the right dorsolateral prefrontal cortex varies with the degree of humor perceived. Our results clarified the differential contributions of the neural loci of irony comprehension, enriching our understanding of pragmatic language communication from a social behavior point of view. *Hum Brain Mapp* 35:1167–1178, 2014. © 2013 Wiley Periodicals, Inc.

Key words: amygdala; language; magnetic resonance imaging; social perception; temporal lobe

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*Correspondence to: Yoritaka Akimoto, Department of Functional Brain Imaging, Institute of Development, Aging and Cancer,

Tohoku University; Seiryomachi 4-1, Aoba-ku, Sendai 980-8575, Japan. E-mail: y-akimoto@idac.tohoku.ac.jp

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INTRODUCTION

Verbal irony implies an underlying emotional attitude that differs from the meaning of what is actually said. Comprehension of irony is a representative example of the high-order sociolinguistic abilities of humans. It goes beyond literal understanding, integrating various types of information from the social context, including events, the speaker's beliefs and emotional attitudes, and paralinguistic cues such as facial expression.

Several studies demonstrate a close relationship between the understanding of irony and theory of mind, which is the ability to attribute mental states to others (Channon et al., 2005, 2007; Creusere, 2000; Dews et al., 1996; Happé, 1993; Harris and Pexman, 2003). Previous functional MRI (fMRI) studies (Eviatar and Just, 2006; Prat et al., 2012; Rapp et al., 2010; Shibata et al., 2010; Spotorno et al., 2012; Uchiyama et al., 2006, 2012; Wang et al., 2006a,b; Wakusawa et al., 2007) found that irony comprehension activates the mentalizing network (Frith and Frith, 2003, 2006), including the medial prefrontal cortex (mPFC) and the temporal regions. At the same time, other studies suggested that deficits in theory of mind may not be the only reason for poor comprehension of irony (Martin and McDonald, 2005; Mo et al., 2008; Monetta et al., 2009; Shamay-Tsoory et al., 2005a,b). Utsumi (2000) reviewed the previous representative theories of irony (Clark and Gerrig, 1984; Grice, 1975; Sperber and Wilson, 1998) and argued that irony comprehension depends on mental conceptual knowledge of verbal irony, in addition to theory of mind ability. Theoretically, theory of mind alone is not sufficient to enable irony comprehension because it cannot discriminate between irony and other types of nonliteral utterances (e.g., metaphors; Utsumi, 2000). Developmental evidence also supports this idea (Pexman and Glenwright, 2007), and further suggests that conceptual knowledge of irony must be developed through social experience with irony. Children understand the false beliefs of others by age 4–5 years (Happé, 1995), yet understanding of irony develops from this only later (Dews et al., 1996; Hancock et al., 2000; Harris and Pexman, 2003; Keenan and Quigley, 1999). Usage of irony in family conversations helps children develop an understanding of irony (Recchia et al., 2010), and children's knowledge of irony is elaborated with age (Filippova and Astington, 2008; Laval and Bert-Eboul, 2005; Pexman et al., 2005). The constraint-satisfaction model (Akimoto et al., 2012; Katz, 2005; Pexman, 2008) provides a good explanation of the respective roles of mentalizing and conceptual knowledge during irony comprehension. In this model, utterance comprehension is achieved through competition among possible interpretations, constrained by multiple interpretive cues from the social context. If interpretive cues support a certain interpretation, that interpretation receives more activation, and the other interpretive possibilities become less active. Thus, this model explains that irony is comprehended through activation of the individual's conceptual knowl-

edge of irony. Theory of mind plays a role in the understanding of context through inferences about the speaker's belief to provide interpretive cues.

Affective aspects are also important because they are not only involved in the processing of emotional interpretive cues, but are also closely related to the social function of irony, which is the reason why irony is used. Irony achieves various communicative goals in social interaction: to express the negative emotional attitude of the speaker (Utsumi, 2000), to draw the listener's attention (Kumon-Nakamura et al., 1995), to be humorous (Toplak and Katz, 2000), and to dilute condemnation (Dews and Winner, 1995; Dews et al., 1995). Humor is an element of the politeness strategy (Brown and Levinson, 1987) used to establish comfortable relationships (Holmes, 2000; Holmes and Stubbe, 2003).

We investigated the neural mechanism of irony comprehension in detail. Specifically, we focused on two important (but previously overlooked) issues: conceptual knowledge of irony and emotional response elicited in the listener. In previous studies, irony was always accompanied by a particular contextual setting that biased ironic interpretation, while the control condition did not contain a contextual cue (Eviatar and Just, 2006; Prat et al., 2012; Rapp et al., 2010; Shibata et al., 2010; Spotorno et al., 2012; Uchiyama et al., 2006, 2012; Wakusawa et al., 2007; Wang et al., 2006a,b). This means that the understanding of context (situational meaning) and irony comprehension *per se* were contaminated. Thus, we separated the effects of the understanding of context to identify the region of the brain underlying the conceptual knowledge of irony. Specifically, even though there are particular situations biasing ironic interpretation, if the speaker is unaware of these situations, then the listener does not have a reason to believe that the utterance was ironic. This approach has been used in psychology studies (Akimoto et al., 2012; Gibbs et al., 1995; Keysar, 1994), but to our knowledge, we are the first to apply it in a brain imaging study. We also analyze data reflecting the emotion evoked in the listener. More specifically, we explore the brain regions modulated by the degree of perceived irony, negative emotion, and humor. This investigation is needed because each instance of irony elicits a different emotion; the same instance of irony may even elicit different emotions in different individuals. To maximize the emotional response in the subjects as listeners, we used a first-person view and a situationally rich story in which irony was directed toward the subject. Moreover, an explicit irony detection task was not employed so that subjects would not focus solely on whether an utterance constitutes irony.

Based on the previous findings, we made the following hypothesis: (1) Conceptual knowledge of irony is represented by the anterior superior temporal gyrus (aSTG), which represents social concepts (Ross and Olson, 2010; Zahn et al., 2007, 2009a,b); (2) perceived irony is associated with activation in the amygdala, because of its known modulation by emotional arousal (Zald, 2003) and because

it plays an important role in affective processing of negative and positive stimuli (Garavan et al., 2001); (3) the degree of negative emotion is associated with activation of the insula (Wicker et al., 2003); and (4) humor is associated with activation in the medial orbitofrontal cortex (Goel and Dolan, 2001), based on its known involvement in reward or affective value (Rolls and Grabenhorst, 2008).

MATERIALS AND METHODS

Subjects

Thirty-five healthy, right-handed, Japanese subjects participated in this study. The sample included 18 men and 17 women, aged 18–23 (mean 20.2) years. All subjects had normal or corrected-to-normal vision; none had a history of neurological or psychiatric illness. Handedness was evaluated using the Edinburgh Handedness Inventory (Oldfield, 1971). Written informed consent was obtained according to the guideline of the Declaration of Helsinki (1991). This study was approved by the ethics committee of Tohoku University Graduate School of Medicine.

Stimuli

We used 80 stories comprised of pictures and sentences to describe daily verbal interactions among three people (“you,” a man, and a woman). The study subject was the listener of the target statement and was represented as “you.” The study subject was always in the story because the story was told from a first-person viewpoint. The presence of people was represented by pictures of their faces. Each story described interactions among friends. Individual characters appeared in only one story each to avoid the influence of familiarity with the characters’ personalities when moving from one story to another. Facial expressions were neutral or slightly smiling and did not change. The facial pictures expanded in size when the person made a comment to help the subject identify who was speaking. Pictures without sentences were also included to help the subject determine who was and who was not present.

Each story consisted of three phases: an introduction, a result, and a target statement (Fig. 1). In the introduction phase, the subject (“you”) said that “you” would do something. This comment implied a positive expectation of the event (e.g., the comment implied that “you” are good enough to ski in the advanced course). After that, one of the characters (the man or the woman) left and therefore remained unaware of the results of “your” actions. In the result phase, the result of the subject’s action (“your action”) was described as success or failure in the absence of the person who had left. In the target statement phase, the scene changed, and one of the characters (the man or the woman) made a comment to “you” with an apparently positive meaning.

Each story had four possible conditions: intentional irony, incongruity without ironic intention, literal state-

ment, or a “filler” statement. In the intentional irony condition, the result of the subject’s action was failure; the speaker was aware of this, so the target statement was intentionally ironic. In the incongruity version, the result of the subject’s action was also failure, but the speaker did not know this; thus, the target statement was intentionally literal, based on his/her positive expectation arising from the prior interaction during the introduction phase (e.g., the speaker believes you are good enough to ski in the advanced course). In the literal version, the result of the subject’s action was success; the speaker was aware of this, and so the target statement was intentionally literal. In the filler version, the result of the subject’s action was success, but the speaker was unaware of this, and so the statement was intentionally literal. The target statements were identical among the conditions; thus, the linguistic stimulus was controlled for the different interpretive scenarios. Ten additional examples of the dialogues used in our study are provided in Supporting Information, Document 1. A preliminary survey was conducted for screening purposes. Ten subjects read each version of the 80 stories and were more than 80% accurate in deciding whether the statements contained irony. Subjects were randomly assigned to 1 of 4 lists that were created to counterbalance the story conditions.

Tasks

Before the main fMRI experiment, subjects assessed eight practice stories following the same approach used in the preliminary survey, then performed the fMRI task with eight practice stories. The main experiment consisted of four fMRI sessions, each of which contained 20 trials (five trials for each condition). Subjects were instructed to interpret the conditions as if they were “you” in the stories. After each story, subjects were asked whether they would make a modest reply to the last target statement. This was a dummy task designed to maintain the subjects’ alertness during the scan. Making a modest reply is a natural (but not obligatory) response to praise among Japanese people (e.g., Japanese tend to say, “No, I am not as good of a skier as you just said,” when their skiing skill is complimented by someone).

Each picture that was accompanied by a sentence was presented for 3 s, except during the result phase, when it was presented for 5 s. Each picture not accompanied by a sentence was presented for 1 s. After the target statement phase, a fixation was presented for 2 s, and then the visual cue was presented for 3 s, during which subjects were asked whether they would make a modest reply by pressing a key. The inter-trial interval was jittered from 1500 to 3500 ms.

Immediately after the fMRI experiment, the stories were shown again and subjects were asked to judge whether the intention of the speaker of each target statement was ironic or literal, and also to rate the perceived degrees of irony, humor, and negative emotion on a scale of 1 (*low*) to 7 (*high*) at their own pace. While judging the intention of the speaker,

Figure 1.

Examples of stimuli. This example describes a skiing situation. The stories were comprised of an (a) introduction phase, (b) result phase, (c) target statement phase, and (d) judgment phase. The irony condition included a failed result and a statement by a friend who saw the results. The incongruity condition was comprised of a failed result and

it was correct for subjects to answer that the statement was literal in the incongruity condition, because we asked about the intention of the speaker, not the perception of the listener. Subjects were instructed to form their answers based on their comprehension during the fMRI experiment rather than their comprehension after re-reading the stories. In the instructions, we used the word “hiniku,” which is the closest semantic match to “irony” in Japanese. We told the subjects to think of “hiniku” as not only aggressive but also characterized by nuanced humor, because “hiniku” has critical connotations compared with “irony” (Okamoto, 2006). Finally, brief, open-ended interviews were conducted, and we checked on the subjects’ levels of alertness during the fMRI scans.

Functional MRI

Forty transaxial gradient-echo images were obtained using the following parameters: echo time, 30 ms; flip angle, 80°;

a statement by a friend who did not see the results. The literal condition involved a successful result and a statement by a friend who saw the results. The filler condition included a successful result and a statement by a friend who did not see the results. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

slice thickness, 2.5 mm; slice gap, 0.5 mm; field of view, 192 mm; matrix, 64 × 64. The images encompassed the entire cerebrum and were acquired at a repetition time of 2.5 s using an echo planar sequence and a 3-T Philips Achieva MR scanner. Each subject completed four scanning sessions. A total of 289 volume images were acquired per session.

Preprocessing procedures and whole-brain analysis were performed using the Statistical Parametric Mapping (SPM5) software package (Wellcome Department of Imaging Neuroscience, London, UK) implemented in the MATLAB R2007a operating environment (MathWorks, Natick, MA, USA). The procedures were as follows: adjustment of acquisition timing across slices, correction for head movement, spatial normalization of each subject’s first echo planar image (EPI) to the EPI template, and smoothing using a Gaussian kernel with full width at half-maximum of 8 mm.

We excluded data from two subjects with head motion greater than 3 mm, four subjects who fell asleep, one

subject who judged the intention of the speaker with less than 80% accuracy, and three subjects who displayed strong egocentric tendencies, failing to identify the speaker's intention in all incongruity trials during one or more of the sessions. Thus, we included data from 25 subjects (11 men and 14 women) in the final analysis.

fMRI Data Analysis

We analyzed the event-related fMRI data by means of two conventional 2-level approaches, using a subtraction method and parametric modulation. First, statistical predictors were generated by convolving a canonical hemodynamic response function provided by SPM5 with the common introduction phase (13-s duration), successful event result (5-s duration), failed event result (5-s duration), target statement correctly identified in the irony condition (3-s duration), target statement correctly identified in the incongruity condition (3-s duration), target statement correctly identified in the literal condition (3-s duration), target statement of no interest (target statements incorrectly identified or the filler condition; 3-s duration), and judgment phase (3-s duration; Supporting Information Fig. 1). A voxel-by-voxel multiple regression analysis of these predictors was applied to the preprocessed images for each subject. Statistical inferences on the contrasts of parameter estimates were performed on the second-level between-subjects (random effects) model using one-sample *t*-tests. The implicit mask image produced by SPM for the random effects analysis is provided in Supporting Information Figure 2, which did not cover a part of the anterior temporal lobes and the orbitofrontal cortex.

To identify the region of the brain representing conceptual knowledge of irony, we compared brain activation during target statements with a contrast between the irony and incongruity conditions (irony–incongruity condition). Our rationale was that context (especially for the speaker's belief) must be considered during the inference of the speaker's intention both in the irony and in the incongruity conditions. Thus, we expect that these effects should be subtracted in the irony–incongruity contrast. To examine the effect of figuring out whether the speaker knows the truth (the result of the event), a contrast between the literal and incongruity conditions (literal–incongruity condition) was also evaluated. We also used a contrast between the irony and literal conditions (irony–literal condition) that had been commonly used in previous studies but might suffer from contamination related to the subject's understanding of context. The activation profiles at the peak voxels of each activation region were also identified. In addition, the contrast between the ironically and non-ironically biasing situations (failure–success) was examined. We did not include the filler condition in any contrast, because some subjects reported that they felt uncomfortable in this condition during the post-fMRI interviews. Because this uncomfortableness was not reported in the preliminary survey for stimulus screening, it seems to come from the de-

cision making of a modest reply in this condition (that is, they might be slightly puzzled whether they should make a modest reply in this case).

Second, parametric modulation was used to investigate the neural correlates of the affective aspect of irony comprehension. We modeled the target statements (including those that were incorrectly identified in the assessment of the intention) across the irony, incongruity, and literal conditions as a single model of parametric modulation that we used as a statistical predictor. This model was composed of responses with the same event timings but with amplitudes correlated with the parameters of interest. Using this model, we identified the activity linearly modulated by the degree of perceived irony (low = 1, high = 7). We also checked negative modulation (low = 7, high = 1). The other statistical predictors (introduction phase, successful event result, failed event result, target statement of no interest, and judgment phase) were used in a manner similar to the first analysis. Activity associated with the degree of negative emotion and humor was also examined in the same way. We excluded 1 subject who assigned the same humor score to all the stories from these analyses.

The voxels were thresholded at $p < 0.001$ (uncorrected) and then corrected to $p < 0.05$ by using the cluster size (Friston et al., 1994).

RESULTS

Comprehension and Rating of Irony

Correct identification of the intention of the target statements, degree of perceived irony, degree of negative emotion, and degree of humor were analyzed using one-way repeated measures analyses of variance (ANOVA) for the effect of condition. As summarized in Table I, the main effect of condition was significant for all of these dependent variables. Follow-up comparisons ($p < 0.05$, Bonferroni method) revealed that identification of the intention was lower in the incongruity condition than in the irony and literal conditions. Perception of the degree of irony was the highest in the irony condition (and higher in the incongruity than in the literal condition), and perception of the degree of negative emotion was higher in the irony and incongruity conditions than in the literal condition. Perception of the degree of humor was the highest in the irony condition. In ironic utterances correctly identified in the assessment of the intention ($n = 480$), the degree of perceived irony were correlated with the degree of negative emotion ($r = 0.47$, $p < 0.01$), but not with the degree of humor ($r = -0.06$, *n.s.*).

Functional MRI Data

Statistically significant areas of activation determined by the subtraction method are shown in Table II and Figure 2. The maximal activation in the irony–incongruity contrast was in the right aSTG; for the irony–literal contrast, it

TABLE I. The identification of the intention and ratings of perceived irony, negative emotion, and humor under different test conditions

	Test condition			<i>F</i> -statistic (<i>df</i>)	<i>t</i> -Value	<i>p</i> -Value
	1. Irony	2. Incongruity	3. Literal			
Correct identification of the intention of the speaker (%)	96.2 (5.3)	87.6 (16.5)	98.4 (3.5)	8.37 (2, 24)		<0.01
1 vs. 2					3.08	<0.01
1 vs. 3					0.79	n.s.
2 vs. 3					3.87	<0.01
Perceived irony	6.1 (0.6)	2.4 (1.1)	1.6 (0.5)	272.03 (2, 23)		<0.01
1 vs. 2					17.96	<0.01
1 vs. 3					21.88	<0.01
2 vs. 3					3.92	<0.01
Negative emotion	5.1 (1.0)	4.7 (1.4)	1.5 (0.5)	126.02 (2, 23)		<0.01
1 vs. 2					1.31	n.s.
1 vs. 3					14.36	<0.01
2 vs. 3					13.05	<0.01
Humor	4.2 (1.1)	2.5 (1.0)	2.2 (0.9)	35.50 (2, 23)		<0.01
1 vs. 2					6.58	<0.01
1 vs. 3					7.85	<0.01
2 vs. 3					1.27	n.s.

Results for identification of the intention are presented as the mean percentage of correct identifications (SD). All rating results are presented as mean (SD) of scores assigned by study subjects under different test conditions. Statistical results of one-way repeated measures ANOVAs and post hoc pairwise comparisons (uncorrected *p*-values and *t*) are also shown.

was in the right anterior inferior temporal gyrus (aITG) and in the right mPFC. For the literal–incongruity contrast, no significant regions were found. For the failure–success contrast, there was activation in the mPFC, bilateral aITG, bilateral middle temporal gyri, and bilateral temporoparietal junction.

Parametric modulation analyses revealed modulation in the right amygdala/hippocampus/parahippocampal gyrus as a positive linear function of the degree of perceived

irony and modulation in the right dorsolateral prefrontal cortex (dlPFC) as a positive linear function of the degree of humor (Table III and Fig. 3). No significant modulation was found in the other parametric modulation analyses.

DISCUSSION

We investigated the neural mechanism of irony comprehension in detail. Our first focus was on identifying the

TABLE II. Significant brain activation determined via the subtraction method for each test condition contrast

	Right or left side	<i>x</i>	<i>y</i>	<i>z</i>	<i>t</i> -Value	Cluster size (mm ³)
Target statement phase						
<i>Irony–incongruity</i>						
Anterior superior temporal gyrus	R	54	6	–21	4.92	2241
<i>Irony–literal</i>						
Medial prefrontal cortex	R	18	54	39	4.89	1755
Anterior inferior temporal gyrus	R	45	–6	–39	4.51	2133
Result phase						
<i>Failure–success</i>						
Medial prefrontal cortex	R	6	48	39	5.90	3537
Anterior inferior temporal gyrus	R	45	3	–39	7.25	6480
	L	–51	0	–36	6.02	4347
Middle temporal gyrus	R	57	–24	–18	6.14	3618
	L	–54	–24	–15	5.36	2268
Temporoparietal junction	R	57	–48	21	5.49	2808
	L	–60	–60	24	5.16	2214

Coordinates, *t*-values of peak activation, and cluster sizes are shown for each activated area. The voxels were thresholded at *p* < 0.001 (uncorrected) and then corrected to *p* < 0.05 by using the cluster size. Coordinates are listed in Montreal Neurological Institute (MNI) stereotactic space.

Figure 2.

Significant regions of activation determined by the subtraction method and activation profiles. (a) The irony–incongruity contrast revealed activation in the right anterior superior temporal gyrus (aSTG). (b) The irony–literal contrast showed activation in the right anterior inferior temporal gyrus (aITG) and the right medial prefrontal cortex (mPFC). (c) Activation for the failure–success contrast during the results phase was observed in the mPFC, bilat-

eral aITG, bilateral middle temporal gyri, and bilateral temporo-parietal junction. The voxels were thresholded at $p < 0.001$ (uncorrected) and then corrected to $p < 0.05$ by using the cluster size. Activation profiles (parameter estimates) during the target statement phase at cluster peaks of (d) the right aSTG (54, 6, –21), (e) the right mPFC (18, 54, 39), and (f) the right aITG (45, –6, –39) are also shown. Error bars indicate standard deviations.

brain region that represents the conceptual knowledge of irony, separating the effects of contextual understanding. We identified the right aSTG as the region responsible for the representation of social conceptual knowledge of irony. We also identified contributions from the mPFC and the aITG in the irony–literal contrast, but not in the irony–incongruity contrast, suggesting that they are involved in understanding of context. Our second focus was the neural correlates of the affective aspects of irony comprehension. We identified modulation of activation in the right amygdala, hippocampus, and parahippocampal gyrus by the degree of perceived irony, which might underlie the mechanism for the social function of irony. Unexpectedly, we

also observed modulation of activity in the right dlPFC by the subject's perception of the degree of humor.

Comprehension and Rating of Irony

Ratings of the perceived degree of irony suggest that the speaker's intention is an important feature defining irony. Even when there is an incongruity between the situation and the literal meaning of the actual words, statements were not perceived as highly ironic when the speaker had no ironic intention. Another interesting finding was that the incongruity and irony conditions evoked negative

TABLE III. Regions of the brain showing positive linear modulation associated with perception of humor and irony

Region	Right or left side	x	y	z	t-Value	Cluster size (mm ³)
<i>Degree of perceived irony</i>						
Amygdala/Hippocampus/Parahippocampal gyrus	R	21	−6	−24	5.58	1431
<i>Degree of humor</i>						
Dorsolateral prefrontal cortex	R	57	33	18	4.90	2052

Coordinates, *t*-values of peak activation, and cluster size are shown for each activated area. See the footnote of Table 2 for information regarding the statistical threshold.

Coordinates are listed in Montreal Neurological Institute (MNI) stereotactic space.

emotion, but humor was not detected in the incongruity condition. This suggests that negative emotion was evoked regardless of whether irony was intended by the speaker, yet humor was derived by evaluating the speaker's ironic intention. The positive correlation between the degree of irony and negative emotion suggested that sense of irony is driven by emotional intensity, as argued by Utsumi (2000).

Social Conceptual Knowledge of Irony

We identified the right aSTG as being responsible for representing social conceptual knowledge of irony.

Although a previous meta-analysis study (Bohrn et al., 2012) revealed that the brain regions most robustly involved in irony comprehension were the mPFC and the right aSTG, there have been few discussions on the role of the right aSTG during irony comprehension. Because the literal–incongruity contrast showed no significant effects, the activation observed in the irony–incongruity contrast was not related to the mechanism of figuring out whether the speaker knows the truth. Our result is consistent with the notion that the aSTG is a neural correlate of social conceptual knowledge and supports social cognition (Ross and Olson, 2010; Zahn et al., 2007). It is thus in line with

Figure 3.

Regions of the brain associated with perception of humor and irony. Parametric modulation analyses revealed positive linear modulation (a) in the right amygdala, hippocampus, and parahippocampal gyrus by the degree of perceived irony, and (b) in the right dorsolateral prefrontal cortex by the degree of humor. See the legend of Figure 2 for information regarding the statistical threshold. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

psychological studies highlighting the importance of empirical social knowledge of irony (Filippova and Astington, 2008; Laval and Bert-Eboul, 2005; Pexman et al., 2005; Pexman and Glenwright, 2007). Our interpretation could also explain the findings of Wang et al. (2006b), in which adults showed greater activation in the superior temporal gyrus during irony comprehension than did children, and those of Rapp et al. (2010), in which a negative association between schizotypal personality traits and activation in the middle temporal gyrus was found during comprehension of irony. Children and those who have schizotypal personalities may have limited available conceptual knowledge of irony.

Context and Theory of Mind

Our observation of activation in the mPFC and the aITG in the irony–literal contrast is consistent with previous reports of their involvement in the comprehension of irony (Eviatar and Just, 2006; Prat et al., 2012; Rapp et al., 2010; Shibata et al., 2010; Spotorno et al., 2012; Uchiyama et al., 2006, 2012; Wang et al., 2006a,b; Wakusawa et al., 2007; note that some of them did not report activation in aITG). However, these activation patterns do not appear to be specific to ironic speech. This idea is also supported by the fact that the mPFC and the temporal pole are involved in various types of mentalizing processes (Frith and Frith, 1999, 2003, 2006; Mitchell et al., 2005; Olson et al., 2007; Singer, 2006; Sugiura et al., 2009). For example, Sugiura et al. (2009) showed that the mPFC and the temporal pole play a role in detecting situational meaning from a picture without a linguistic stimulus. Indeed, we observed activation of the mPFC and the aITG in the failure–success contrast, which might correspond to the understanding of the prerequisite situational setting of irony (Utsumi, 2000). Visser et al. (2010) argued that aITG processes all levels of concept, based on the activation in the aITG during semantic categorization task where basic level concepts and categories were used as stimuli. This might be the reason why its involvement is not specific to ironic speech, which has a higher load on social conceptual knowledge. Together, these regions seem to be involved in processing the understanding of context, which provides interpretive cues.

Emotion and the Degree of Irony

We identified a modulation of activity in the right amygdala based on the degree of irony perceived. Kipps et al. (2009) found that decreased grey matter volume in the right amygdala is associated with poor understanding of irony among patients with frontotemporal dementia, suggesting that the amygdala plays a role in the decoding of ironic messages. Thus, although our observations suggested that the amygdala was sensitive to the listener's emotional states rather than the intention of the speaker, we interpreted that this sensitivity might result from successful communication between speaker and listener, in which speaker–listener neural coupling might occur (Stephens et al., 2010). These neural

processes might be an underlying mechanism of the social function of irony, i.e., expressing the speaker's emotional attitude (Utsumi, 2000) and drawing the listener's attention (Kumon-Nakamura et al., 1995). The cluster found to be linearly modulated by the perceived degree of irony also includes the hippocampus and parahippocampal gyrus, which are important for memory (Eichenbaum et al., 2007; Squire et al., 2004). Emotionally arousing information is well-remembered (McGaugh et al., 1996; McGaugh, 2004; Phelps, 2004; Richter-Levin, 2004), and the underlying mechanism for this may be co-activation of the hippocampus and amygdala during successful encoding of emotional information (Murty et al., 2010). Thus, our results are consistent with previous behavioral studies in which irony is sometimes remembered better than literal expression (Gibbs, 1986a,b; Kreuz et al., 1991; Pexman and Olineck, 2002).

Humor and the Right dIPFC

We observed a modulation of activity in the right dIPFC influenced by the degree of humor perceived. Brain lesion studies consistently suggested that the right frontal cortex is necessary for humor perception (Wild et al., 2003; Gardner et al., 1975; Shammi and Stuss, 1999). The dIPFC is an important region for executive function and is involved in the understanding of humorous stimuli, probably because the understanding of humor imposes cognitive demands for the resolution of incongruence (Azim et al., 2005; Shammi and Stuss, 1999). Strick et al. (2009) showed that humorous stimuli posing greater cognitive demands attenuate negative emotions. Thus, the observed activation in the dIPFC might also be an underlying neural correlate of the social functions of irony, i.e., to be humorous (Toplak and Katz, 2000) and to dilute condemnation (Dews and Winner, 1995; Dews et al., 1995). Another possible interpretation is that the right PFC activation represents suppression of emotional expression (i.e., smiling) in response to humor (Wild et al., 2006). However, our stimulus did not seem to be funny enough to motivate a smile, as shown by the high rating scores of negative emotion associated with irony.

The lack of activation in the medial orbitofrontal cortex might be due to magnetic susceptibility artifacts. Actually, the location of the activities in the medial orbitofrontal cortex reported by Wakusawa et al. (2007) was not covered in our analysis, maybe due to signal loss caused by inhomogeneities in the magnetic field, which occurs near air/tissue interface (Schmithorst et al., 2001; Visser et al., 2010; Weiskopf et al., 2006). Another possibility is that irony did not work as a reward in our study, because it alluded to the failure of a person who was a virtual proxy for the subjects in this study.

Pragmatic Language Communication as Social Behavior

Our study also contributes the understanding of pragmatic language communication as a social behavior

beyond irony comprehension. Holtgraves (2008) argues that listeners automatically recognize the speech acts (Austin, 1962; Searle, 1969, 1975, 1979) that speakers performed with their utterances. A speech act is a summary of the speaker's intentions, for example, to warn, to offer, to thank the listener, or to be ironic (Haverkate, 1990). Through adequate conceptual knowledge of speech act, people are able to understand a speaker's intentions effectively without a full analysis of each remark in a real-time communication. Understanding of a speaker's intentions leads to emotional responses in the listener. Our results identify several key regions that may provide a mechanistic substrate for enabling emotional responses and emotional communication between the speaker and listener. Emotional communication is important to establish and maintain comfortable relationships in social life. Our results, which demonstrate a complex mechanism of pragmatic language comprehension, may help formulate a detailed understanding of the poor (and likely diverse) pragmatic communicative abilities of children, brain-damaged people, autistic patients, and schizophrenic patients. Further, our results are generally consistent with the framework of moral cognition (Moll et al., 2005), which consist of three main components: contextual event representation, provided by the PFC; social conceptual knowledge, stored in the anterior temporal cortex; and basic emotional states, which depend on cortical-limbic circuits. Thus, our study might also contribute to the understanding pragmatic language communication from the point of view of social behavior.

Methodological Consideration

There is an important issue to be discussed in regard to stimulus control. There are two typical ways of controlling stimuli in irony studies. One is to use the same situation (The room is actually messy) with different target statements (e.g., "Your room is so clean!" vs. "Your room is so messy!"; Gibbs, 1986a), in which the emotion induced by the situation is controlled, but the sentence itself is not. The other is to use the same target statements (e.g., "Your room is so clean!") in different situations (e.g., the room is actually clean vs. messy; Giora et al., 1998), as was done in our irony-literal contrast. In this case, the sentence is controlled, while the connotation and emotion induced from the situation are not.

Using either of these two control strategies, one can control for the sentence or the connotation/emotion, but not both. Our irony-incongruity contrast avoided this tradeoff by controlling both sentence and situation simultaneously. Although emotional connotation intended by the speaker and whether the failure was public to the speaker were still not matched, we think it is unlikely that these factors produced critical impact on our results for two reasons. First, our results on emotion were based on parametric modulation analysis, which is independent from the con-

trol of emotion among conditions. Second, if these factors exerted a great influence, we would expect them to also influence the listener's emotion. However, the emotion perceived by the listener was similarly negative in both condition, and negative emotion showed no significant effect in the parametric modulation analysis. Zahn et al. (2007) also reported that activation in the aSTG is independent of emotional valence.

CONCLUSION

Activation in the right aSTG is specifically involved in the understanding of irony, which reflects social conceptual knowledge of irony. The mPFC and the aITG may contribute to the comprehension of irony through understanding of context (situational meaning), but their contribution may not be specific to irony. Modulation of activity in the right amygdala, hippocampus, and parahippocampal gyrus is associated with the degree of irony perceived, and modulation of activity in the right dlPFC varies with the degree of humor perceived. These neural mechanisms of emotional communication are closely related to the social function and purpose of irony.

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REFERENCES

- Akimoto Y, Miyazawa S, Muramoto T (2012): Comprehension processes of verbal irony: The effects of salience, egocentric context, and allocentric theory of mind. *Metaphor Symb* 27:217–242.
- Austin JL (1962): *How to Do Things with Words*. Oxford, UK: Oxford University Press.
- Azim E, Mobbs D, Jo B, Menon V, Reiss AL (2005): Sex differences in brain activation elicited by humor. *Proc Natl Acad Sci U S A* 102:16496–16501.
- Bohnm 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* 50:2669–2683.
- Brown P, Levinson S (1987): *Politeness: Some Universals in Language Usage*. Cambridge, UK: Cambridge University Press.
- Channon S, Pellijeff A, Rule A (2005): Social cognition after head injury: Sarcasm and theory of mind. *Brain Lang* 93:123–134.
- Channon S, Rule A, Maudgil D, Martinos M, Pellijeff A, Frankl J, Drury H, Shieff C (2007): Interpretation of mentalistic actions and sarcastic remarks: Effects of frontal and posterior lesions on mentalising. *Neuropsychologia* 45:1725–1734.
- Clark HH, Gerrig RJ (1984): On the pretense theory of irony. *J Exp Psychol Gen* 113: 121–126.
- Creusere MA (2000): A developmental test of theoretical perspectives on the understanding of verbal irony: Children's

- recognition of allusion and pragmatic insincerity. *Metaphor Symb* 15:29–45.
- Dews S, Kaplan J, Winner E (1995): Why not say it directly? The social functions of irony. *Discourse Process* 19:347–367.
- Dews S, Winner E (1995): Muting the meaning: A social function of irony. *Metaphor Symb Act* 10:3–19.
- Dews S, Winner E, Kaplan J, Rosenblatt E, Hunt M, Lim K, McGovern A, Qualter A, Smarsh B (1996): Children's understanding of the meaning and functions of verbal irony. *Child Dev* 67:3071–3085.
- Eichenbaum H, Yonelinas AP, Ranganath C (2007): The medial temporal lobe and recognition memory. *Annu Rev Neurosci* 30:123–152.
- Eviatar Z, Just MA (2006): Brain correlates of discourse processing: An fMRI investigation of irony and conventional metaphor comprehension. *Neuropsychologia* 44:2348–2359.
- Filippova E, Astington JW (2008): Further development in social reasoning revealed in discourse irony understanding. *Child Dev* 79:126–138.
- Friston KJ, Worsley KJ, Frackowiak RSJ, Mazziotta JC, Evans AC (1994): Assessing the significance of focal activations using their spatial extent. *Hum Brain Mapp* 1:210–220.
- Frith CD, Frith U (1999): Interacting minds: A biological basis. *Science* 286:1692–1695.
- Frith U, Frith CD (2003): Development and neurophysiology of mentalizing. *Philos Trans R Soc Lond B Biol Sci* 358:459–473.
- Frith CD, Frith U (2006): The neural basis of mentalizing. *Neuron* 50:531–534.
- Garavan H, Pendergrass JC, Ross TJ, Stein EA, Risinger RC (2001): Amygdala response to both positively and negatively valenced stimuli. *Neuroreport* 12:2779–2783.
- Gardner H, Ling PK, Flamm L, Silverman J (1975): Comprehension and appreciation of humorous material following brain damage. *Brain* 98:399–412.
- Gibbs RW (1986a): On the psycholinguistics of sarcasm. *J Exp Psychol Gen* 115:3–15.
- Gibbs RW (1986b): Comprehension and memory for nonliteral statements: The problem of sarcastic indirect requests. *Acta Psychol* 62:41–57.
- Gibbs RW, O'Brien JE, Doolittle S (1995): Inferring meanings that are not intended: Speakers' intentions and irony comprehension. *Discourse Process* 20:187–203.
- Giora R, Fein O, Schwartz T (1998): Irony: Graded salience and indirect negation. *Metaphor Symb* 13:83–101.
- Goel V, Dolan RJ (2001): The functional anatomy of humor: Segregating cognitive and affective components. *Nat Neurosci* 4:237–238.
- Grice HP (1975): Logic and conversation. In: P. Cole and J. Morgan, eds., *Syntax and semantics*, vol. 3: *Speech acts*. New York: Academic Press. p 41–58.
- Hancock JT, Purdy K, Dunham PJ (2000): Children's comprehension of critical and complimentary forms of verbal irony. *J Cogn Dev* 1:227–248.
- Happé FG (1993): Communicative competence and theory of mind in autism: A test of relevance theory. *Cognition* 48:101–119.
- Happé FG (1995): The role of age and verbal ability in the theory of mind task performance of subjects with autism. *Child Dev* 66:843–855.
- Harris M, Pexman PM (2003): Children's perceptions of the social functions of verbal irony. *Discourse Process* 36:147–165.
- Haverkate H (1990): A speech act analysis of irony. *J Pragmat* 14:77–109.
- Holmes J (2000): Politeness, power and provocation: How humour functions in the workplace. *Discourse Studies* 2:159–185.
- Holmes J, Stubbe M (2003): Power and politeness in the workplace: A sociolinguistic analysis of talk at work. London, Longman.
- Holtgraves T (2008): Automatic intention recognition in conversation processing. *J Mem Lang* 58:627–645.
- Katz AN (2005): Discourse and sociocultural factors in understanding nonliteral language. In: Colston H, Katz AN, editors. *Figurative Language Comprehension: Social and Cultural Influences*. Mahwah, NJ: Lawrence Erlbaum Associates, Inc. pp183–207.
- Keenan TR, Quigley K (1999): Do young children use echoic information in their comprehension of sarcastic speech? A test of echoic mention theory. *Brit J Dev Psychol* 7:83–96.
- Keysar B (1994): The illusory transparency of intention: Linguistic perspective taking in text. *Cogn Psychol* 26:165–208.
- Kipps CM, Nestor PJ, Acosta-Cabronero J, Arnold R, Hodges JR (2009): Understanding social dysfunction in the behavioural variant of frontotemporal dementia: The role of emotion and sarcasm processing. *Brain* 132:592–603.
- Kreuz RJ, Long DL, Church MB (1991): On being ironic: Pragmatic and mnemonic implications. *Metaphor Symb Act* 6:149–162.
- Kumon-Nakamura S, Glucksberg S, Brown M (1995): How about another piece of pie: The allusional pretense theory of discourse irony. *J Exp Psychol Gen* 124:3–21.
- Laval V, Bert-Eboul A (2005): French-speaking children's understanding of sarcasm: The role of intonation and context. *J Speech Lang Hear Res* 48:610–620.
- Martin I, McDonald S (2005): Evaluating the causes of impaired irony comprehension following traumatic brain injury. *Aphasiology* 19:712–730.
- McGaugh JL, Cahill L, Roozendaal B (1996): Involvement of the amygdala in memory storage: Interaction with other brain systems. *Proc Natl Acad Sci U S A* 93:13508–13514.
- McGaugh JL (2004): The amygdala modulates the consolidation of memories of emotionally arousing experiences. *Annu Rev Neurosci* 27:1–28.
- Mitchell JP, Banaji MR, Macrae CN (2005): The link between social cognition and self-referential thought in the medial prefrontal cortex. *J Cogn Neurosci* 17:1306–1315.
- Mo S, Su Y, Chan RC, Liu J (2008): Comprehension of metaphor and irony in schizophrenia during remission: The role of theory of mind and IQ. *Psychiatry Res* 157:21–29.
- Moll J, Zahn R, de Oliveira-Souza R, Krueger F, Grafman J (2005): Opinion: The neural basis of human moral cognition. *Nat Rev Neurosci* 6:799–809.
- Monetta L, Grindrod CM, Pell MD (2009): Irony comprehension and theory of mind deficits in patients with Parkinson's disease. *Cortex* 45:972–981.
- Murty VP, Ritchey M, Adcock RA, LaBar KS (2010): fMRI studies of successful emotional memory encoding: A quantitative meta-analysis. *Neuropsychologia* 48:3459–3469.
- Okamoto S (2006): Perception of Hiniku and Oseji: How hyperbole and orthographically deviant styles influence irony-related perceptions in the Japanese language. *Discourse Process* 41:25–50.
- Oldfield RC (1971): The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia* 9:97–113.
- Olson IR, Plotzker A, Ezzyat Y (2007): The enigmatic temporal pole: A review of findings on social and emotional processing. *Brain* 130:1718–1731.

- Pexman PM, Olineck KM (2002): Does sarcasm always sting? Investigating the impact of ironic insults and ironic compliments. *Discourse Process* 33:199–217.
- Pexman PM, Glenwright M, Krol A, James T (2005): An acquired taste: Children's perceptions of humor and teasing in verbal irony. *Discourse Process* 40:259–288.
- Pexman PM, Glenwright M (2007): How do typically developing children grasp the meaning of verbal irony? *J Neurolinguistics* 20:178–196.
- Pexman PM (2008): It's fascinating research: The cognition of verbal irony. *Curr Dir Psychol Sci* 17:286–290.
- Phelps EA (2004): Human emotion and memory: Interactions of the amygdala and hippocampal complex. *Curr Opin Neurobiol* 14:198–202.
- Prat CS, Mason RA, Just MA (2012): An fMRI investigation of analogical mapping in metaphor comprehension: The influence of context and individual cognitive capacities on processing demands. *J Exp Psychol Learn Mem Cogn* 38:282–294.
- 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* 113:1–12.
- Recchia HE, Howe N, Ross HS, Alexander S (2010): Children's understanding and production of verbal irony in family conversations. *Br J Dev Psychol* 28:255–274.
- Richter-Levin G (2004): The amygdala, the hippocampus, and emotional modulation of memory. *Neuroscientist* 10:31–39.
- Rolls ET, Grabenhorst F (2008): The orbitofrontal cortex and beyond: from affect to decision-making. *Prog Neurobiol* 86:216–244.
- Ross LA, Olson IR (2010): Social cognition and the anterior temporal lobes. *Neuroimage* 49:3452–3462.
- Schmithorst VJ, Dardzinski DJ, Holland SK (2001): Simultaneous correction of ghost and geometric distortion artifacts in EPI using a multi-echo reference scan. *IEEE Trans Med Imag* 20:535–539.
- Searle J (1969). *Speech Acts*. Cambridge, UK: Cambridge University Press.
- Searle J (1975). Indirect speech acts. In Cole P, Morgan, J (Eds.), *Syntax and Semantics 3: Speech Acts*. New York: Academic Press, pp 59–82.
- Searle J (1979). *Expression and Meaning*. Cambridge, UK: Cambridge University Press.
- Shamay-Tsoory SG, Tomer R, Berger BD, Goldsher D, Aharon-Peretz J (2005a): Impaired “affective theory of mind” is associated with right ventromedial prefrontal damage. *Cogn Behav Neurol* 18:55–67.
- Shamay-Tsoory SG, Tomer R, Aharon-Peretz J (2005b): The neuro-anatomical basis of understanding sarcasm and its relationship to social cognition. *Neuropsychology* 19:288–300.
- Shammi P, Stuss DT (1999): Humour appreciation: A role of the right frontal lobe. *Brain* 122:657–666.
- Shibata M, Toyomura A, Itoh H, Abe J (2010): Neural substrates of irony comprehension: A functional MRI study. *Brain Res* 1308:114–123.
- Singer T (2006): The neuronal basis and ontogeny of empathy and mind reading: Review of literature and implications for future research. *Neurosci Biobehav Rev* 30:855–863.
- Sperber D, Wilson D (1998): Irony and relevance: A reply to Seto, Hamamoto and Yamanashi. In: R. Carston and S. Uchida, eds., *Relevance theory: Applications and implications*. Amsterdam: Benjamins. p 283–293.
- Spotorno N, Koun E, Prado J, Van Der Henst JB, Noveck IA (2012): Neural evidence that utterance-processing entails mentalizing: The case of irony. *Neuroimage* 63:25–39.
- Squire LR, Stark CE, Clark RE (2004): The medial temporal lobe. *Annu Rev Neurosci* 27:279–306.
- Stephens GJ, Silbert LJ, Hasson U (2010): Speaker-listener neural coupling underlies successful communication. *Proc Natl Acad Sci U S A* 107:14425–14430.
- Strick M, Holland RW, van Baaren RB, van Knippenberg A (2009): Finding comfort in a joke: consolatory effects of humor through cognitive distraction. *Emotion* 9:574–578.
- Sugiura M, Wakusawa K, Sekiguchi A, Sassa Y, Jeong H, Horie K, Sato S, Kawashima R (2009): Extraction of situational meaning by integrating multiple meanings in a complex environment: A functional MRI study. *Hum Brain Mapp* 30:2676–2688.
- Toplak M, Katz AN (2000): On the uses of sarcastic irony. *J Pragmat* 32:1467–1488.
- 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* 1124:100–110.
- Uchiyama HT, 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* 48:563–583.
- Utsumi A (2000): Verbal irony as implicit display of ironic environment: Distinguishing ironic statements from nonirony. *J Pragmat* 32:1777–1806.
- Visser M, Embleton KV, Jeffries E, Parker GJ, Lambon Ralph MA (2010): The inferior, anterior temporal lobes and semantic memory clarified: Novel evidence from distortion-corrected fMRI. *Neuropsychologia* 48:1689–1696.
- Wakusawa K, Sugiura M, Sassa Y, Jeong H, Horie K, Sato S, Yokoyama H, Tsuchiya S, Inuma K, Kawashima R (2007): Comprehension of implicit meanings in social situations involving irony: A functional MRI study. *Neuroimage* 37:1417–1426.
- 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* 129:932–943.
- Wang AT, Lee SS, Sigman M, Dapretto M (2006b): Developmental changes in the neural basis of interpreting communicative intent. *Soc Cogn Affect Neurosci* 1:107–121.
- Weiskopf N, Hutton C, Josephs O, Deichmann R (2006): Optimal EPI parameters for reduction of susceptibility-induced BOLD sensitivity losses: A whole-brain analysis at 3T and 1.5T. *Neuroimage* 33:493–504.
- Wicker B, Keysers C, Plailly J, Royet JP, Gallese V, Rizzolatti G (2003): Both of us disgusted in my insula: The common neural basis of seeing and feeling disgust. *Neuron* 40:655–664.
- Wild B, Rodden FA, Grodd W, Ruch W (2003): Neural correlates of laughter and humour: A review. *Brain* 126:2121–2138.
- Wild B, Rodden FA, Rapp A, Erb M, Grodd W, Ruch W (2006): Humor and smiling: Cortical regions selective for cognitive, affective, and volitional components. *Neurology* 66:887–893.
- Zahn R, Moll J, Krueger F, Huey ED, Garrido G, Grafman J (2007): Social concepts are represented in the superior anterior temporal cortex. *Proc Natl Acad Sci U S A* 104:6430–6435.
- Zahn R, Moll J, Iyengar V, Huey ED, Tierney M, Krueger F, Grafman J (2009a): Social conceptual impairments in frontotemporal lobar degeneration with right anterior temporal hypometabolism. *Brain* 132:604–616.
- Zahn R, Moll J, Paiva M, Garrido G, Krueger F, Huey ED, Grafman J (2009b): The neural basis of human social values: Evidence from functional MRI. *Cereb Cortex* 19:276–283.
- Zald DH (2003): The human amygdala and the emotional evaluation of sensory stimuli. *Brain Res Brain Res Rev* 41:88–123.