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ARTICLE

The role of the amygdala in incongruity resolution: the case of humor comprehension

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ABSTRACT
A dominant theory of humor comprehension suggests that people understand humor by first perceiving some incongruity in an expression and then resolving it. This is called "the incongruity-resolution theory." Experimental studies have investigated the neural basis of humor comprehension, and multiple neural substrates have been proposed; however, the specific substrate for incongruity resolution is still unknown. The reason may be that the resolution phase, despite its importance in humor comprehension, has not been successfully distinguished from the perception phase because both phases occur almost simultaneously. To reveal the substrate, we conducted a functional magnetic resonance study using 51 healthy participants. We used a humor-producing frame of "Given *A*, I'd say *B*, because *C*" so as to focus on the resolution phase independently by suspending humor processing just after the perception phase. This frame allowed us to separate the two phases. Based on our results, incongruity resolution evoked positive emotion and activated the left amygdala, which is known to be related to positive emotion. On the basis of these findings, we argue that the amygdala plays an important role in humor comprehension, considering its functional role in emotional evaluation, particularly the relevance detection for incoming stimuli.

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Humor comprehension; amygdala; incongruity resolution; relevance detector; fMRI

Introduction

Humor involves a positive emotion, a cognitive process, and a social context (Martin, 2007), and is a unique human characteristic (Goel & Dolan, 2001). Telling a joke, a witty comment, or a self-deprecating episode can suddenly strike us as humorous (Martin, 2007). This phenomenon has been investigated for many centuries in a wide variety of disciplines, including philosophy, psychology, and linguistics. Recent studies have focused on the process of humor comprehension, and assumed that an expression that elicits humor is processed in phases. This idea is encompassed by the incongruity-resolution theory (Attardo, Hempelmann, & Di Maio, 2002; Forabosco, 1992; Suls, 1972; Wyer & Collins, 1992).

The perception of incongruity occurs in the first phase, but it does not yet elicit humor. Prior to the first phase, initial assumptions are formed. In other words, the listener makes assumptions based on the context of the story (Hurley, Dennett, & Adams, 2011). The listener then perceives various incongruities that contrast with the initial assumptions, such as something that is different from the ordinary (Forabosco, 1992). There may also be ambiguity or incoherence (Attardo et al., 2002), as shown in the following example:

> O'Riley was on trial for armed robbery. The jury came out and announced, "Not guilty." "Wonderful," responded O'Riley. "Does that mean I can keep the money?" (Suls, 1972, p. 90).

The last part is something different from an ordinarily expected reaction and suggests that O'Riley is (actually) guilty, which creates an incoherence.

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The resolution of incongruity occurs in the second phase, and it elicits humor. The incongruity is resolved when a new relationship is found to fill the gap (Hillson & Martin, 1994; Mio & Graesser, 1991) or when a mistake in the initial assumptions is noted (Hurley et al., 2011). In the above example, a mistake is found. Specifically, O'Riley is not (actually) innocent, but is (legally) not guilty. The phrase "My surgeon is a butcher among doctors" (Mio & Graesser, 1991, p. 95) is an example of finding a new relationship. This example uses the metaphorical expression "*A* is *B*," where a literal interpretation is not possible (Hillson & Martin, 1994; Mio & Graesser, 1991). In other words, the relevant relationship between surgeon and butcher is seemingly difficult to understand at first, even though we have assumptions regarding both the surgeon and the butcher. This situation creates incongruity because the intended phrase "because *C*" is not explicitly expressed. This allows the listener to search for some covertly expressed relationships (Hillson & Martin, 1994). In this respect, a feature of metaphorical expression is creating new relationships. One example is that both the surgeon and the butcher cut off flesh. This is where the humor occurs if and only if there is positive emotional valence. Thus, the resolution phase is an important phase in that it is where humor elicitation takes place. In this phase, there must be a common feature between finding a new relationship and finding a mistake.

Considering that positive emotion is involved in the resolution phase of incongruity, the common feature between finding a new relationship and finding a mistake may be an emotional evaluation (specifically relevance detection) of the findings (Sander, Grafman, & Zalla, 2003). Sander et al. (2003) suggested that "an event is relevant for an organism if it can significantly influence (positively or negatively) the attainment of his or her goals, the satisfaction of his or her needs, the maintenance of his or her own well-being, and the well-being of his or her species" (p. 311). For example, if a student in medical school hears "My surgeon is a butcher among doctors" (Mio & Graesser, 1991, p. 95) and finds a new relationship between surgeon and butcher, the student may change his or her area of specialty. If a good person believes that O'Riley is (actually) not guilty in the above-mentioned example and offers assistance to him against the false accusation, then he may suffer of physical damage from him. However, if the good person realizes that O'Riley is not (actually) innocent, then he can prevent this damage. This view is also applicable to other theories of humor. According to the superiority theory of humor (Hobbes, 1840), a factor important to humor is "sudden glory arising from some sudden conception of some eminency in ourselves, by comparison with the infirmity of others, or with our own formerly" (p. 46). According to the release theory of humor (Spencer, 1859), humor is "a form of relief from excessive nervous arousal" (Hurley et al., 2011, p. 44), especially sexual and aggressive drives, which would normally be repressed. These can significantly influence one's well-being. These theories suggested that humor processing is related to positive emotion, but did not mention incongruity resolution as a humor-specific processing. Thus, relevance detection (Sander et al., 2003) may be an important feature of humor comprehension.

Previous experimental studies have investigated the neural basis of humor comprehension and have proposed multiple neural substrates; however, there is no consensus on the area that is specific to the resolution of incongruity (Vrticka, Black, & Reiss, 2013a). Sander et al. (2003) have suggested that the amygdala plays a role in relevance detection. This view has been supported by experimental studies, such as personal relevance of emotional faces (Strathearn & Kim, 2013), social relevance of verbal stimuli (Bestelmeyer, Belin, & Ladd, 2015; Schirmer et al., 2008), and a tendency of greater social relevance than personal relevance in situational pictures (Vrticka, Sander, & Vuilleumier, 2012). Some studies have suggested that the amygdala is related to the process of finding a new relationship (Amir, Biederman, Wang, & Xu, 2015) or finding a mistake (Levens, Devinsky, & Phelps, 2011; Levens & Phelps, 2010). It is well known that the amygdala is related to positive emotion (Hamann & Mao, 2002; Herbert et al., 2009; Sander et al., 2003) and is one of the most frequently reported neural substrates in humor processing (Vrticka et al., 2013a). We thus hypothesized that the amygdala is specifically involved in the resolution of incongruity.

The lack of consensus regarding the specific substrate for incongruity resolution is probably due to the fact that previous experimental studies of neural substrates have not successfully distinguished between the perception phase and the resolution phase. Indeed, the two phases are likely to occur continuously and there is no clear behavioral transition marker to differentiate between them (Vrticka et al., 2013a). To investigate our hypothesis, we devised an experimental design exclusively focusing on the resolution phase of incongruity by suspending the humor comprehension process immediately after the perception phase of incongruity. We then analyzed the resolution phase as the target phase using functional magnetic resonance imaging (fMRI). Specifically, we used a form of metaphorical expression in which humor may occur following the discovery of a new relationship (Hillson & Martin, 1994; Mio & Graesser, 1991). Support of our hypothesis suggests that the amygdala must be activated in all previous studies of humor. To investigate the reported frequency of amygdala activation in previous studies, we also conducted a meta-analysis using the related literature.

Methods

Participants

For our fMRI study, 51 participants were recruited as paid volunteers (23 women and 28 men; mean age, 22.5 years; range, 18–37 years). All participants had normal or corrected-to-normal visual acuity, and were right-handed (mean score, 82.8; range, 25–100) according to the Edinburgh handedness inventory (Oldfield, 1971). No history of neurological or psychiatric illness was identified. All participants had at least a high school education level. Written informed consent to participate in this study was obtained following procedures approved by the Ethical Committee of the National Institute for Physiological Sciences, Japan. The experiments were undertaken in compliance with national legislation and the Code of Ethical Principles for Medical Research Involving Human Subjects of the World Medical Association (Declaration of Helsinki).

Preparation of task materials

To examine whether the amygdala is specifically involved in the resolution of incongruity in humor comprehension when the two phases are separated, we formulated our experimental design so that there was only incongruity resolution in the target stimuli. We modified the context so that identical target stimuli provoked either incongruity resolution or no resolution. This is a context-controlled identical target stimuli method with an event-related design (Harada et al., 2009; Mano, Harada, Sugiura, Saito, & Sadato, 2009; Uchiyama et al., 2012). In other words, by using "*A* is *B*," which is a form of metaphorical expression wherein humor can occur (Hillson & Martin, 1994; Mio & Graesser, 1991), we controlled the difficulty of finding a new relationship in order to suspend the humor comprehension process immediately after the perception phase of incongruity. We then overtly expressed the intended relationship "because *C*", as it is difficult for the listener to find it by himself or herself. Thus, we also controlled the new relationship used to elicit humor.

Instead of using the "*A* is *B*, because *C*" expression as is, we transformed it into "Given *A*, I'd say *B*, because *C*," because this structurally equal expression is familiar to Japanese participants in this experiment. Specifically, we used a Japanese riddle called "nazokake," which is expressed in the following format: "(1) *A* to kakete, (2) *B* to toku, (3) sono kokoro wa, (4) *C* (dakara)." This Japanese riddle format permits us to identify four different stages. We treat the first three stages as the context phase and the fourth stage as the target phase when we study the comprehension process of humor, as follows:

(1) The first stage introduces a concept ("Given the concept of *A* [e.g., savings]").
(2) The second stage introduces another concept ("I'd say *B* [e.g., my wife's smile]").
(3) The third stage asks whether the listener knows some relationship between the two concepts ("Do you know why they are similar?"). In many cases, the listener (reader) fails to find the relationship. This means that the perception of incongruity arises, but the resolution process is suspended.
(4) The fourth stage provides the rationale for the intended connection ("Because *C* [e.g., if they disappear, I will be in trouble]"). This is where the resolution of the incongruity occurs.

The first three stages are structurally equal to "savings are my wife's smile," a typical form of metaphorical expression. In other words, an expression with two concepts permitting neither a literal interpretation nor the discovery of a new relationship in an ordinary manner is presented in the first three stages. Comprehension is thus suspended. When the relationship is provided in the fourth stage, the expression becomes now understandable and can be interpreted as "If my savings disappear, I will be in trouble" and "If my wife's smile disappears, I will be in trouble." In other words, only the resolution phase of the incongruity occurs in the target phase. This is an important distinction from previous studies (Chan, Chou, Chen, & Liang, 2012; Chan et al., 2013) where both the perception and the resolution phases occur in the same target phase. If the newly found relationship is accompanied by positive emotional valence, then we consider it a humorous expression. In order to reveal this effect, we set a baseline (i.e., non-humorous expression) that is accompanied by neither a newly found relationship nor positive emotional valence. As we explain in more detail later, to check for the presence or absence of a newly found relationship and positive emotional valence, we asked the participants to select the best reason for their humorous judgment from a set of options after the fMRI session.

The riddles were gleaned from Nakamura (2009) and Google Internet searches (http://google.com). Using the collected riddles, we selected humorous candidates. We then altered the second concept

("*B*") of each riddle to create non-humorous candidates. We made 44 pairs of humorous and non-humorous stimuli, where the humor depended on the value for *B*. We were thus able to cancel out any effects due to target stimuli differences.

To reject badly paired stimuli, eight normal volunteers (4 women and 4 men; mean age, 27.0 years; range, 22–44 years) participated in a pilot study. The number of participants was minimal because this study was used to select strict stimuli for analysis by the participants undergoing fMRI. Stimuli were discarded from the list when one of the pair was judged as humorous by less than three participants, or when the other stimulus was judged as non-humorous by less than three participants. Of the 24 paired stimuli from Nakamura (2009), eight pairs were rejected based on these criteria. We produced another 20 pairs of stimuli using Google internet searches. Two of these pairs were also excluded based on above criteria. We thus had a total of 34 pairs (i.e., humorous and non-humorous candidates) of test items in this study (see Table S1 in the supplementary appendix).

fMRI procedures

Prior to the fMRI session, the participants received detailed instructions regarding the task procedures and were trained using training stimuli not used during the fMRI session. All stimuli were prepared and presented using Presentation® 14.8 software (Neurobehavioral Systems, Albany, CA) running on a personal computer (Dimension® 9200; Dell Inc., Round Rock, TX). Using a liquid crystal display projector (DLA-M200L; Victor, Yokohama, Japan), the visual stimuli were projected onto a half-transparent viewing screen located behind the head coil of the MRI scanner. The participants viewed the stimuli via a mirror attached to the head coil. The spatial resolution of the projector was 1,024 × 768 pixels, with a 60-Hz refresh rate. The distance between the screen and the participant's eyes was approximately 60 cm, and the visual angle was 18.9° (horizontal) × 14.2° (vertical). The sentence stimuli (maximum visual angle, 7.8° × 0.9°) were written in Japanese and presented in white letters on a black background.

In each trial (see Figure 1), the first stage, "Given the concept of *A*," was presented on the screen for 1.5 seconds, followed by a fixation cross (visual angle, 0.6° × 0.6°) for 1.25 seconds. The second stage, "I'd say *B*," lasted for 2 seconds and was followed by a fixation cross for 1.25 seconds. The third stage, "Do you know why they are similar?" lasted for 0.75 seconds and was followed by a fixation cross for 1.75 seconds. Finally, the fourth stage, "Because *C*," lasted for 3.5 seconds, and was followed by a fixation cross for 2 seconds. A fixed inter-stimulus interval was used because an identical inter-stimulus interval was

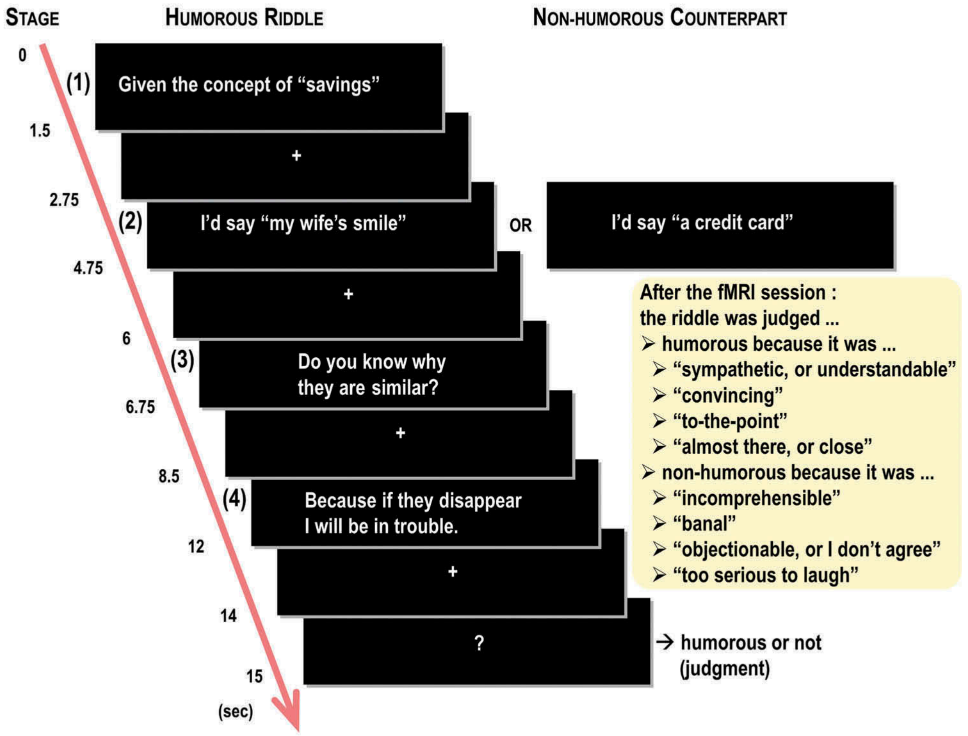

Figure 1. The time course of the experiment with an example. We used the first three stages as a context phase and the fourth stage as a target phase. In the humorous stimuli, the perception of incongruity arises during the context phase, while the resolution of incongruity occurs at the target phase. On the other hand, in the non-humorous one, no resolution occurs.

unlikely to affect the difference in evoked humor caused by a context-controlled identical target stimuli method (Harada et al., 2009; Mano et al., 2009; Uchiyama et al., 2012). The length of each stage was set to correspond to the maximum length of the presented stimuli. The participants were then instructed to judge whether the riddle was humorous by pressing a button to make their choice after the presentation of a question mark (visual angle, 0.6° × 0.6°) for 1 second then a fixation cross for 5 seconds.

We used an event-related design to minimize habituation and learning effects. The 34 paired stimuli were presented in a pseudorandom order. During one of two runs, each with 17 humorous candidates and 17 non-humorous candidates, the run order was counterbalanced across the participants to cancel out the effects of the same participants reading paired stimuli.

All images were acquired using a 3-Tesla MR scanner (Allegra®; Siemens, Erlangen, Germany). An ascending T2*-weighted gradient-echo echo-planar imaging (EPI) procedure was used to produce 34 continuous trans-axial slices covering the entire cerebrum and the cerebellum (repetition time [TR], 2,000 ms; echo time [TE], 30 ms; flip angle, 85°; field of view [FoV], 192 mm; 64 × 64 matrix; voxel dimensions, 3.0 × 3.0 mm in plane; 4.0-mm slice thickness with 15% gap). Oblique scanning was used to exclude the eyeballs from the images. Each run consisted of a continuous series of 354 volume acquisitions for a total duration of 11 minutes and 48 seconds. T1-weighted magnetization prepared-rapid acquisition gradient echo (MP-RAGE) images were also obtained for anatomical imaging (TR, 2,500 ms; TE, 4.38 ms; flip angle, 8°; FoV, 230 mm; 1 slab; number of slices per slab, 192; voxel dimensions, 0.9 × 0.9 × 1.0 mm) for each participant.

After the fMRI session, the participants were asked to select the best reason for their judgment from a set of options (Nakamura, 2009), a procedure which enabled us to check the features of the judgments using the factor “newly found relationship” (i.e., newly found or not) and the factor “positive emotional valence” (i.e., positive or not). The options provided as reasons for judging a riddle to be humorous included the following: I take the riddle in question to be “sympathetic or understandable (*maa kyokan-suru*),” “convincing (*naru-hodo to nattoku-suru*),” “to-the-point (*umai to unaru*; i.e., strongly humorous),” or “almost there or close (*oshii*; i.e., weakly humorous)”. If the expression was somewhat humorous but its relationship was found in the context phase, the option “almost there or close” was instructed to be selected. In other words, this fourth option was indicated for cases accompanied by a positive emotional valence without a newly found relationship, while the other three options were indicated for cases accompanied by both a newly found relationship and a positive emotional valence. The reasons provided for judging a riddle to be non-humorous included the following: I take the riddle in question to be “incomprehensible (*wakaranai*),” “banal (*atarimae*),” “objectionable or I do not agree (*naiyou-teki-ni igi-ari*),” or “too serious to laugh (*shin-koku sugi-te warae-nai*).” If the expression was incomprehensible or banal, there was neither a newly found relationship nor a positive emotional valence. On the other hand, the other two options are indicative of cases accompanied by a newly found relationship without positive emotional valence. It took approximately 60 minutes for each participant to complete the experiment.

Data analysis

Performance data analysis

In this study, selection of strict stimuli for the analysis was conducted on the judgment of fMRI participants. Thirty-four paired stimuli of humorous (h) and non-humorous stimulus (n) were presented and evaluated by the participants during fMRI experiment. Previous studies (Chan et al., 2012; Goel & Dolan, 2001) asked to judge whether the expression was humorous or non-humorous in the fMRI scanner. Thus, we used this judgment and calculated the rating of humorousness in each stimulus based on the measurement with multiple participants. Across 51 participants of the fMRI experiments, we defined the humorousness of a stimulus as the ratio of the participants judging the stimulus to be humorous relative to all the participants (range, 0.0 to 1.0; Rh, humorousness of h; Rn, humorousness of n). The large difference pair was defined as $Rh > 0.5$ and $Rn < 0.5$. The tiny-difference pair was thus defined as $Rh \leq 0.5$ or $Rn \geq 0.5$. We conducted a chi-square test for frequencies in a 2 (“candidate,” i.e., humorous candidates [h] *versus* non-humorous candidates [n] based on the results of the pilot study) × 2 (“humorous judgment,” i.e., judged to be humorous *versus* non-humorous by the fMRI participants) cross table of each pair. If its result was not significant (*n.s.*), the pair was regarded as the tiny-difference pair. Table S1 in the appendix presented the detailed information regarding the humorousness of all 34 pairs of stimuli. Of the set of 34 paired stimuli, 19 large-difference pairs of H (humorous stimulus) and N (non-humorous counterpart) were selected and used for the subsequent imaging data analysis. The remaining

15 tiny-difference pairs were distinguished from the *H* and *N* pairs in the data analysis in that they had a smaller significant difference, with the pairs *H′* (stimulus which was judged to be more humorous than its counterpart in the pair of *h* and *n*) and *N′* (stimulus that was judged to be less humorous than its counterpart in the pair of *h* and *n*).

To study the nature of the large-difference pairs using the two conditions (*H* and *N*), a paired *t* test was conducted on the angular transformed ratio (i.e., ratio with arcsine square root transformation that transformed a data set to a normal distribution) of the participants judging the stimulus to be humorous relative to all participants, as a main analysis. As a post hoc analysis used to describe the relationship between large-difference pairs and tiny-difference pairs using the four conditions (*H, N, H′*, and *N′*), a two-way ANOVA with two within-participant factors, "selection" (i.e., large-difference pairs or not) and "humorousness" (i.e., humorous or not), was conducted on the angular transformed ratio of the participants judging the stimulus to be humorous relative to all participants. For the large-difference pairs, we also conducted a 2 ("humorousness") × 8 ("reasons") ANOVA within participants on the angular transformed ratio of each reason selected, with a Bonferroni's correction for multiple comparisons. These analyses were carried out using SPSS® version 22.0 software (IBM, Armonk, NY).

fMRI data analysis

We preprocessed the imaging data. The first six EPI volumes from each run were discarded due to unsteady magnetization, and the remaining 348 EPI volumes per run (for a total of 696 EPI volumes per participant) were analyzed using Statistical Parametric Mapping 12 (SPM12; Wellcome Department of Imaging Neuroscience, London, UK; Friston, Ashburner, Kiebel, Nichols, & Penny, 2007) implemented in MATLAB® (Mathworks, Natick, MA). EPI volumes were spatially realigned to correct for head motion. They were also corrected for differences in slice timing within each volume. T1-weighted anatomical images were then co-registered to the mean images of the EPI volumes, segmented into gray and white matter, reconstructed using a signal inhomogeneity correction procedure, and spatially normalized to the Montréal Neurological Institute (MNI) T1 template. The normalization parameters of the T1-weighted anatomical image were applied to all of the EPI volumes and then spatially smoothed in three dimensions using an 8-mm full-width at half-maximum Gaussian kernel.

After preprocessing, we analyzed the EPI data for each participant using a general linear model. The target phases for each of the four conditions (*H, N, H′*, and *N′*) were separately modeled. The context phase was modeled as a regressor. Button responses were also modeled as independent regressors. All regressors were convolved with a hemodynamic response function. High-pass filters (128 seconds) were applied to the time-series data. Six regressors for head movement parameters obtained in the realignment process were entered in the model. An autoregressive model was used to estimate temporal autocorrelation. The signals of the EPI images were scaled to a grand mean of 100 overall voxels and volumes within each run.

The contrast images, which consisted of the weighted sum of parameter estimates and represented the normalized task-related increment of the MR signal obtained in the individual analysis, were subjected to subsequent group analysis using a random-effects model in order to make population-level inferences regarding the task-related activation. As a main analysis, data from 51 participants and two contrasts (*H* and *N*) of the large-difference pairs were incorporated into the paired *t* test (Friston et al., 2007). To show activations related to the resolution of incongruity, we created the contrast of ($H - N$). As a post hoc analysis for activation in the contrast of ($H - N$), to show the activation of the large-difference and the tiny-difference pairs, four contrasts (*H, N, H′*, and *N′*) were incorporated into the 2 ("selection") × 2 ("humorousness") within-participant factorial design (Friston et al., 2007). Specifically, using the flexible factorial design model (Friston et al., 2007), a participant factor was set as an independent variable to take into account different individuals. Error variance was set to be equal across participants because they were sampled from the same underlying population. On the other hand, two condition-factors were set as dependent variables because the different factor levels were correlated within participants. We used equal error variances because the data were obtained from the same participants. To check activation for the tiny-difference pairs, the contrast of ($H' - N'$) was created. We also studied the main effect of selection (the contrast of $[H + N] - [H' + N']$), the main effect of humorousness (the contrast of $[H + H'] - [N + N']$), and the interaction between these two factors (the contrast of $[H - N] - [H' - N']$).

The resulting set of voxel values for each contrast constituted a statistical parametric map of the *t* statistic, which was conducted using a correction for multiple comparisons at the peak level with a conservative family-wise error (FWE) threshold of $p < 0.05$ for the entire brain. In the post hoc analysis, an inclusive mask of the activated area(s) in the contrast of ($H - N$) for the paired *t* test was used with the above settings. The activated area was determined by SPM Anatomy Toolbox version 2.1 (Eickhoff et al., 2007).

To check for laterality in the region of interest (ROI), which was significantly activated by the contrast of ($H - N$), we defined an ROI (i.e., left amygdala; size, 1,796 mm^3; max length, 19 × 13 × 17 mm) and a left-right-flipped ROI (i.e., right amygdala; size, 1,984 mm^3; max length, 19 × 15 × 19 mm) using MarsBaR AAL ROIs version 0.2 software, and extracted the ROI data from individual analyses using MarsBaR version 0.44 software (http://marsbar.sourceforge.net). To check for specificity in the ROI, the ROI data of ($H' - N'$) contrasts in individual analyses were also extracted. In total, data from 51 participants across the two ROIs and two conditions were incorporated into the 2 ("selection") × 2 ("laterality") within-participant factorial design using SPSS. To check the relationship between the ROI and the above-mentioned performance data, correlations between the ROI data and performance data from each of the 51 participants were also investigated using SPSS.

Meta-analysis of previous studies

To determine the reported frequency of amygdala activation in previous studies of humor, we conducted a meta-analysis using the related literature. A total of 160 studies published between 1985 and the end of 2016 were identified using a search in PubMed (using the term "humor" along with "fMRI," 144 studies; and using "humor" along with "PET" (positron emission tomography), 17 studies; one study was duplicated). However, many unrelated studies, such as those on parts of human eye, namely "aqueous humor" or "vitreous humor," were contained in our results. We included 132 studies that contained "humor" or "joke" in the title or abstract, and then excluded 68 studies that contained "aqueous" or "vitreous," leaving 64 studies. We finally included 47 studies with original imaging data that were written in English. We thus excluded 17 studies: Six studies on reducing stress using humor during medical care, four studies using the word "humor" to mean "temper," and four review articles. The other studies were about experimental systems, had no imaging data, or were not in English. Subsequently, we conducted coordinate-based meta-analysis using GingerALE 2.3.6 software (Eickhoff et al., 2009) to summarize the most reported neural substrates regarding the humor process. In this analysis, we included 31 studies that contained coordinates by the contrast of humorous *versus* non-humorous or parametric modulation of humorousness. We thus excluded 16 studies: Six studies reporting no coordinate, five having neither contrast of humorous *versus* non-humorous nor parametric modulation of humorousness, three reporting only patients' data, and two morphological studies. Coordinates reported in Talairach space were transformed into MNI coordinates using the "Talairach to MNI (SPM)" tool implemented in GingerALE. For analyses, a threshold of 0.05 (false discovery rate [FDR]), a less conservative mask size, and a minimum volume of 100 mm^3 were chosen (Rapp, Mutschler, & Erb, 2012). We also checked a more conservative threshold of 0.01 (FDR).

Results

Behavioral performance

As mentioned above, a set of 34 humorous stimuli (mean humorousness, 61.7%; range, 19.6–88.2%) and 34 non-humorous stimuli (mean humorousness, 34.8%; range, 9.8–74.5%) were used. However, 15 paired stimuli were "tiny-difference" pairs (i.e., pairs where the difference between humorous and non-humorous was minimal). On the other hand, 19 humorous stimuli (mean humorousness, 69.3%; range, 54.9–88.2%) and 19 non-humorous stimuli (mean humorousness, 26.1%; range, 9.8–45.1%) were "large-difference" pairs (see Table S1 in the appendix; 55.9% of all stimuli; chi-square test of humorousness for each paired stimulus, $p < 0.05$; paired t test of humorousness of all participants for large-difference pairs in the main analysis, $t(50) = 12.512$, $p < 0.001$; see Figure 2) and were used in the subsequent imaging data analysis using a random-effects model. To verify the nature of the selected stimuli (i.e., large-difference pairs), 15 stimuli with greater humorousness in the tiny-difference pairs (mean humorousness, 56.3%; range, 25.5–88.2%) and 15 with less humorousness (mean humorousness, 41.6%; range, 9.8–72.5%) were considered to be tiny-difference pairs. In the post hoc analysis, a two-way ANOVA revealed a significant main effect of the factor "humorousness," i.e., humorous or not, $F(1, 50) = 127.742$, mean squared error (MSE) = 0.043, $p < 0.001$, but no significant main effect of the factor "selection," i.e., large-difference or not was observed, $F(1, 50) = 1.337$, $MSE = 0.019$, *n.s.* There was a significant interaction between these two factors, $F(1, 50) = 55.788$, $MSE = 0.027$, $p < 0.001$. The nature of this interaction was such that in stimuli with greater humorousness in the pairs, the humorousness of the large-difference pairs was greater than that of the tiny-difference pairs, $F(1, 100) = 182.170$, $MSE = 0.035$, $p < 0.001$. However, the humorousness of the large-difference pairs was less than that of the tiny-difference ones in pairs with less humorousness, $F(1, 100) = 17.799$, $MSE = 0.035$, $p < 0.001$. Thus, the difference in humorousness in the large-difference pairs was greater than that in the tiny-difference pairs.

The overall mean ratios of the reasons for the humorous stimuli in the large-difference pairs were as follows: 3.9% for "sympathetic, or understandable," 16.6% for "convincing," 37.0% for "to-the-point," 3.3% for "almost there, or close," 8.9% for "incomprehensible," 6.8% for "banal," 1.0% for

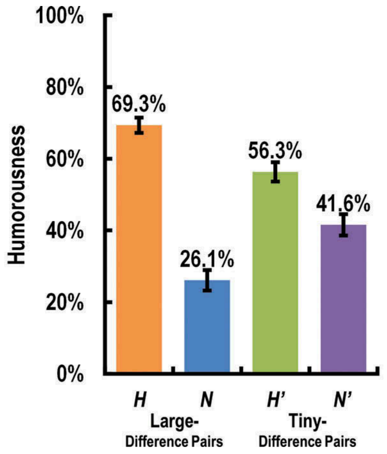

Figure 2. The behavioral results of humorous judgments for large-difference pairs (H, humorous one, and N, non-humorous one), and tiny-difference pairs (H', one with greater humorousness in the pairs, and N', one with less humorousness). Only stimuli pairs were regarded as large-difference pairs, based on if one of the pair was judged humorous by more than half of the functional magnetic resonance imaging (fMRI) participants and the other was judged non-humorous by more than half of the fMRI participants, with a significance in a chi-square test for frequencies in a cross table.

"objectionable, or I do not agree," and 3.3% for "too serious to laugh." In the case of the non-humorous counterparts, we obtained the following results (the mean ratios of the reasons for non-humorous stimuli): 2.8% for "sympathetic, or understandable," 5.3% for "convincing," 2.8% for "to-the-point," 3.5% for "almost there, or close," 21.3% for "incomprehensible," 39.6% for "banal," 1.0% for "objectionable, or I do not agree," and 3.2% for "too serious to laugh." A two-way ANOVA revealed a significant main effect of the factor "humorousness," $F(1, 50) = 8.934$, $MSE = 0.004$, $p < 0.01$, and a significant main effect of the factor "reasons," $F(7, 350) = 37.850$, $MSE = 0.050$, $p < 0.001$. There was a significant interaction between these two factors, $F(7, 350) = 66.709$, $MSE = 0.026$, $p < 0.001$. The nature of this interaction was such that, in the case of humorous stimuli, "to-the-point," $F(1, 400) = 258.562$, $MSE = 0.023$, $p < 0.001$ and "convincing," $F(1, 400) = 38.299$, $MSE = 0.023$, $p < 0.001$, were selected as the main reasons for humorous judgments, meaning that the newly found relationships were accompanied by positive emotional valence. On the other hand, "banal," $F(1, 400) = 190.754$, $MSE = 0.023$, $p < 0.001$ and "incomprehensible," $F(1, 400) = 34.133$, $MSE = 0.023$, $p < 0.001$, were the main reasons for non-humorous judgments in the non-humorous counterparts. This indicates that the baseline was accompanied by neither newly found relationships nor positive emotional valence. The other reasons were not statistically significant. Thus, these effects in the contrast of $(H - N)$ were considered to be canceled out. In other words, the contrast of $(H - N)$ contained the effects of both newly found relationships and positive emotional valence. These effects encompassed the resolution of incongruity in humor comprehension.

Group analysis using a random-effects model

According to the group analysis using a random-effects model, in the main analysis, only left amygdala activation (MNI coordinates [−18 − 8 − 16]; cluster size, 61; peak level statistics: T value 6.604, Z value 5.573, and family-wise error [FWE] of $p < 0.001$; see Figure 3) was found in the large-difference pairs (the contrast of $[H - N]$) using the paired t test for the entire brain. In other words, no other activation was found because the common processes of linguistic humor were canceled out by a context controlled identical target stimuli method. In the post hoc analysis for the activated area in the large-difference pairs, i.e., the left amygdala, no significant activation was found in the tiny-difference pairs (the contrast of $[H' - N']$; see Figure 3). In addition, there was no main effect of selection, humorousness, or an interaction between these two factors. A two-way ANOVA for the two ROIs (bilateral amygdalae) revealed a significant main effect of the factor "selection," i.e., large-difference pairs *versus* tiny-difference pairs, $F(1, 50) = 6.589$, $MSE = 1.213$, $p < 0.05$, and a significant main effect of the factor "laterality," i.e., left *versus* right, $F(1, 50) = 12.278$, $MSE = 0.080$, $p < 0.001$. There was a significant interaction between these two factors, $F(1, 50) = 4.847$, $MSE = 0.160$, $p < 0.05$. The nature of this interaction was such that, in the large-difference pairs, the activation of the left amygdala was greater than that of the right amygdala, $F(1, 100) = 14.608$, $MSE = 0.120$, $p < 0.001$. However, no significant differences were found between the left and the right amygdala, $F(1, 100) = 0.053$, $MSE = 0.120$, *n.s.*, for the tiny-difference pairs. Moreover, in the left amygdala, the activation of the large-difference pairs was greater than that of the tiny-difference pairs, $F(1, 100) = 10.014$, $MSE = 0.686$, $p < 0.01$. However, in the right amygdala, no significant differences were observed between the large-difference pairs and the tiny-difference pairs, $F(1, 100) = 2.758$, $MSE = 0.686$, *n. s.* On the basis of this post hoc analysis, amygdala activation was specific to the large-difference pairs and was significantly left-lateralized. No significant correlation was found between left amygdala activation and the ratio of humorous judgments or the ratio of each reason selected.

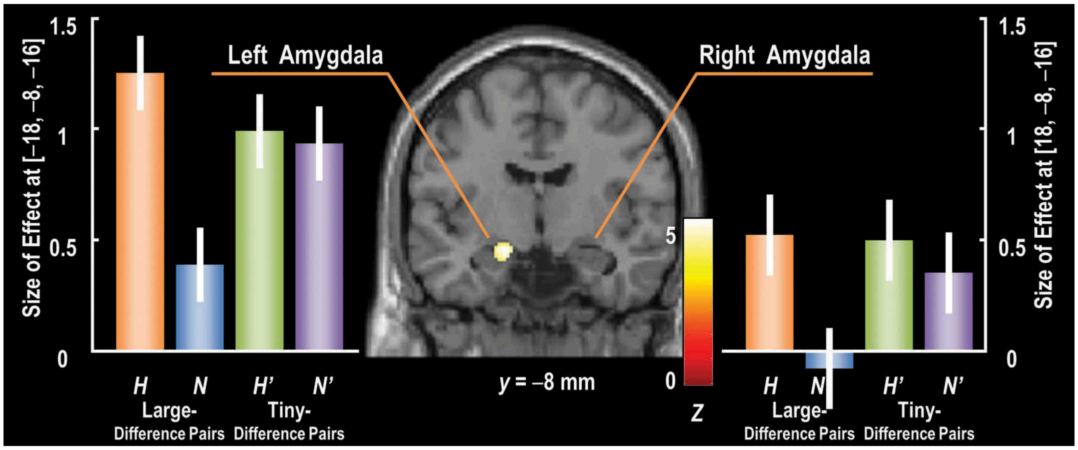

Figure 3. An activation related to incongruity resolution in humor comprehension. As a main analysis, we conducted the paired *t* test for the large-difference pairs (*H*, humorous stimuli; *N*, non-humorous ones). In the contrast of (*H* – *N*), we only found the left amygdala activation (Montréal Neurological Institute [MNI] coordinates [–18 – 8 – 16], family-wise error of $p < 0.05$ as multiple comparisons at the peak level threshold for the entire brain). To show the activation graphs of the large-difference pairs and the tiny-difference pairs (*H′*, stimuli with greater humorousness in the pairs; *N′*, that with less one), we used a post hoc analysis of 2 (the factor "selection," i.e., large-difference pairs or not) × 2 (the factor "humorousness," i.e., humorous or not) within participant factorial design, and found no activation in the tiny-difference pairs (each graph was drawn using the implicit baseline as zero along with the right amygdala [18 – 8 – 16]). Coordinates (*y* mm) are given in MNI space.

Meta-analysis of previous studies

Our coordinatebased meta-analysis revealed four cluster activations (FDR, $p < 0.05$): left amygdala (MNI coordinates [–22 – 2 – 24]; volume size, 704 mm^3; extrema value, 0.029746732), right amygdala ([24 – 4 – 20], 544 mm^3, 0.031029807), and midbrain ([–6 – 20 – 6], 392 mm^3, 0.028337285; [14 – 22 – 10], 168 mm^3, 0.02405684). In a more conservative threshold of 0.01 (FDR), only two clusters remained (coordinates and extrema values were same as above): left amygdala (volume size, 216 mm^3) and right amygdala (184 mm^3).

Based on our frequency based result (see Table S2 in the appendix) and a recent review study (Vrticka et al., 2013a), we suggest that the amygdala is a relevant neural substrate in the humor process.

Discussion

In summary, the analysis of the behavioral data in the large-difference pairs confirmed our predictions regarding the resolution of incongruity and discovering a new relationship (Hillson & Martin, 1994; Mio & Graesser, 1991) accompanied by positive emotional valence. When a newly found relationship was accompanied by positive emotional valence, the expression was judged humorous. On the other hand, when neither a newly found relationship nor positive emotional valence was involved, the expression was judged non-humorous. Thus, the contrast of humorous target stimuli *versus* non-humorous stimuli was due to effects of both a newly found relationship and positive emotional valence.

In this study, the corresponding neural activation was found in the left amygdala. A recent review (Vrticka et al., 2013a) suggested that humor processing consists of both cognitive and emotional components: the cognitive component includes the perception and resolution of incongruity, and the emotional component is mainly represented by the mesocorticolimbic dopaminergic brain areas. Vrticka et al. (2013a) also postulated the amygdala as the linkage node between these components. In addition to the reward-related mechanisms, the functional profile of the amygdala includes a relevance detector (Pessoa & Adolphs, 2010; Sander et al., 2003; Vrticka et al., 2013a). An event is relevant for organisms if it can significantly influence their goals, needs, and well-being (Sander et al., 2003). Because the specificity of emotion relies on the cognitive evaluation of the meaning and the consequence of an event within a particular context and relationship to one's goal (Sander et al., 2003), the detection of relevance is the crucial phase of the emotion processing. The amygdala is attributed a key role in selecting inputs that are most relevant to the organism at a given moment in time. Such "biological value" seems to be prominently related to the processing of salience, significance, ambiguity, and unpredictability (Pessoa & Adolphs, 2010). Accordingly, humor specific processing should activate the amygdala because its function of relevance detection may be involved in incongruity resolution (Vrticka et al., 2013a).

The amygdala, which has generally been considered a modular system used to detect and avoid danger rapidly and automatically, is involved in emotional evaluation (specifically relevance detection) for incoming biological stimuli (Costafreda, Brammer, David, & Fu, 2008; Sander et al., 2003). The amygdala is activated in response to both positive emotional stimuli (e.g., happy faces, pleasant tastes, and erotic films) and negative stimuli (e.g., fearful faces, faces expressing sadness, and angry faces with direct gazes) (Sander et al., 2003). Thus, affective valence, i.e., positive or negative, plays a secondary role (Hamann & Mao, 2002). The amygdala functions not only as a relevance detector for biological stimuli such as faces, gazes, and voices but also as a relevance detector for verbal stimuli; this is especially true for the left amygdala (Hamann & Mao, 2002; Herbert et al., 2009; Sander et al., 2003). Just a word of "his or her species" (Sander et al., 2003, p. 311) can be enough for relevance detection (Herbert et al., 2009). It is suggested that the left amygdala is involved in conscious and cognitively controlled emotional processes, while the right amygdala is involved in unconscious and automatic emotional processes (Dyck et al., 2011; Markowitsch, 1998; Morris, Ohman, & Dolan, 1998). Left amygdala activation in our study may reflect this tendency. It has also been suggested that relevance-based processing may facilitate the salience (Sander, 2012) and arousal network (Raz & Buhle, 2006), which is involved in identifying the most relevant stimuli used to guide behavior (Menon & Uddin, 2010).

Thus, the view that the amygdala is a relevance detector, which plays a role in prioritizing both positive and negative information, has been supported by a number of studies (Bach, Talmi, Hurlemann, Patin, & Dolan, 2011; Ousdal et al., 2008; Sergerie, Chochol, & Armony, 2008). Some reports claim that most sensory information projects onto the amygdala via the dual-route architecture (McDonald, 1998; Pessoa & Adolphs, 2010; Sander et al., 2003). The first route is a direct subcortical pathway that provides coarse information, while the second route is an indirect cortical pathway that provides more refined information. The amygdala is also involved in providing output projections to almost all areas. According to Pessoa and Adolphs (2010), the number of output projections is an important distinction between the amygdala and other neural structures proposed to be involved in relevance detection: the orbitofrontal cortex for discrimination of the valence, anterior cingulate cortex for computing an object's biological value, anterior insula for emotional feelings, and colliculus and pulvinar for filtering out a distractor stimulus. Using extensive output projections, the amygdala coordinates the function of cortical networks during relevance detection (Pessoa & Adolphs, 2010), i.e., emotional resolution (Levens et al., 2011). Among these relevance detection networks, the amygdala, considering its descending connections and its coordinating role (Pessoa & Adolphs, 2010), is the most likely neural substrate involved in incongruity resolution of humor processing.

To segregate the neural substrates of incongruity perception and incongruity resolution during humor comprehension, the nonsensical sentences, which include irresolvable inconsistencies, were used (Chan et al., 2013). The nonsensical sentences activated the right middle temporal gyrus and posterior rostral portion of the medial frontal cortex (prMFC), representing the perception of incongruity. In contrast, humorous sentences activated the anterior rostral portion of the medial frontal cortex (arMFC) and the left inferior parietal lobule. The authors suggested that these areas were related to the resolution of incongruity. These findings are consistent with the neural substrates of pragmatics where the arMFC, which is a critical node of mentalizing, was commonly activated by metaphor and sarcasm sentences (Uchiyama et al., 2012), both of which required the incongruity resolution to be understood (Utsumi, 2000, 2005). Thus, pragmatic incongruity resolution may be represented by neural substrates outside of the traditional language area.

To depict the neural substrates specific to humor processing, Chan et al. (2012) used the garden-path sentences, which require grammatical incongruity resolution processing but do not elicit humor. They found that both humor and garden-path sentences activated the bilateral inferior frontal gyrus, prMFC, and ventral striatum; whereas humor specific activation was observed in the ventromedial prefrontal cortex and bilateral amygdala-parahippocampal gyrus. The results of grammatical incongruity resolution were consistent with the previous study by Uchiyama et al. (2008). According to Chan et al. (2012), however, the incongruity resolution in their experiment appears to have two stages: grammatical and pragmatic. They have shown that humor processing requires more than linguistic disambiguation, and that the amygdala may be the core node for this additional process. Accordingly, we inferred that this additional process is the resolution of pragmatic incongruity by relevance detection.

In humor comprehension, the amygdala, considering its roles as a linking node between cognitive and emotional components (Vrticka et al., 2013a) and in coordinating the function of cortical networks during relevance detection (Pessoa & Adolphs, 2010), seems to be involved in both emotional evaluation (Sander et al., 2003) and emotional resolution (Levens et al., 2011). Thus, it is conceivable that the amygdala was activated by the resolution of (pragmatic) incongruity.

In this respect, our data seem to be consistent with these previous studies and support the incongruity-resolution theory (Attardo et al., 2002; Forabosco, 1992; Suls, 1972).

There are some limitations to this study that should be considered. First, we used sentences as visual stimuli. Thus, further research on the effects of the use of other types of stimuli (e.g., sentences as auditory stimuli, cartoons, or videos) should be carried out within the experimental framework we proposed in this study. Second, the perception phase of incongruity needs to be also investigated with the framework. Third, as the amygdala activation was reported to correlate with introversion (Mobbs, Hagan, Azim, Menon, & Reiss, 2005), the relationship between incongruity resolution and personality-related data may be an additional issue to be investigated. Fourth, our experimental design focused on finding a new relationship; thus, we need to investigate the possible differences between finding a new relationship and finding a mistake in the resolution of incongruity. In addition, distinguishing the effects of the resolution of incongruity and those of positive emotional valence, if both are not tightly coupled in humor comprehension, is an issue to be investigated in the future. Future research should address the above-mentioned limitations in order to identify the specific neural substrate(s) of humor comprehension.

Conclusion

This study contributes to the understanding of humor comprehension by revealing important features of the resolution of incongruity and its potential neural substrate. Previous theoretical studies (Attardo et al., 2002; Forabosco, 1992; Suls, 1972; Wyer & Collins, 1992) suggest that the resolution of incongruity is important. The resolution of incongruity involves finding a new relationship (Hillson & Martin, 1994; Mio & Graesser, 1991) or finding a mistake (Hurley et al., 2011). We hypothesized that relevance detection (Sander et al., 2003) is an important feature and that the amygdala is the specific substrate for the resolution of incongruity. This was supported by our results. The amygdala is involved in coordinating the function of cortical networks during relevance detection (Pessoa & Adolphs, 2010). It is well known that the amygdala, one of the most frequently reported neural substrates, is related to positive emotion (Amir et al., 2015; Hamann & Mao, 2002; Herbert et al., 2009). On the basis of the findings here, we argue that the amygdala plays an important role in humor comprehension.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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