Title

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Journal

Proceedings of the Annual Meeting of the Cognitive Science Society, 34(34)

ISSN

1069-7977

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Publication Date

2012

Peer reviewed

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Abstract

The purpose of this study was to investigate the neuropsychological process and timing of appreciating humor upon reading a set of Japanese riddles which were made up of 4 distinct phases: "Given A (1st phase), I'd say B (2nd phase). Do you know why? (3rd phase) It is because X (4th phase)." To investigate how the brain responds when an individual finds the answer to the riddle ("It is because X") humorous, this study used the fMRI method. We found that when a participant judged the answer to the riddle humorous, the bilateral amygdalae had been significantly activated at the 4th phase. When the participant judged the answer to the riddle banal (non-humorous), by contrast, the left amygdala was found to be significantly activated earlier at the 3rd phase. Therefore, we argue that in both cases, activation of the amygdala is related to the detection of optimal relevance.

Keywords: amygdala; detection of optimal relevance; fMRI; process of humor appreciation; Relevance Theory.

Introduction

Timing control is essential for a type of Japanese riddle in the following example, which has the fixed form of "Given A (target word), I'd say B (response word). Do you know why? (question) It is because X (answer)" ("A *to kakete*, B *to toku, sono kokoro wa*, X.").

"Given 'the savings,' I'd say 'a smile of my wife'. Do you know why? It is because if they disappear, I will be in trouble."

In this sequence of utterances, two seemingly unrelated items were mentioned by the speaker and the hearer is expected to reason how on earth they are connected. The process of mentally searching for the connection and discovering it finally on the basis of the rationale provided by the speaker yield humorous effects. The sequence has four distinctive phases: the 1st phase introduces the target concept ("Given A"); the 2nd phase introduces the response concept ("I'd say B"); the 3rd phase asks the hearer if he knows the rationale for making connection between the two concepts ("Do you know why?"); and the 4th phase provides the rationale for the supposed connection ("It is because X"). In this functional magnetic resonance imaging (fMRI) study, we presented a set of such sequences to participants, and then asked them to judge whether or not the given riddles are humorous after they heard the rationale.

Incongruity resolution in humor appreciation

According to a standard humor appreciation model (Suls, 1972; Wyer & Collins, 1992; Yus, 2003; Martin, 2006), incongruities in the content of the utterance must be identified and resolved for it to be humorous. The incongruities are typically caused by violation of a set of expectations stored in "mental schemas" which are "formed on the basis of past experience with objects, scenes, or events and consists of a set of (usually unconscious) expectations about what things look like and/or the order in which they occur" (Mandler, 1979, p. 263). Thus, in humor appreciation, the simultaneous activation of two incompatible schemas is essential (Wyer & Collins, 1992).

In the Japanese riddle, it is structurally controlled. During the 1st and the 2nd phase, two different schemas corresponding to a target word and a response word are likely to be activated. Two incompatible schemas are simultaneously activated between the 2nd and the 4th phase. When incongruities between these schemas are noticed, the hearer of the riddle naturally looks for a novel and interesting way to resolve them. When a rationale for connecting the two seemingly unrelated concepts is provided at the 4th phase, the incongruities get resolved. At that point, the two existing incompatible schemas and a new schema corresponding to the rationale given are likely to be activated simultaneously. The success of the humor relies upon this resolution being inaccessible before it is given, yet obvious with hindsight when given. If either the resolution fails to be logically coherent or is instead too obvious, the riddle is judged banal.

According to Relevance Theory (Matsui, 2000; Sperber & Wilson, 1995; Yus, 2003; Utsumi, 2005), the motivation for appreciating humor comes from search for "relevance," which is a property of inputs to cognitive processes and is determined by the balance between the cognitive effect and processing effort. An input has cognitive effect if it significantly improves a cognitive environment of an individual. In order to process the input, though, some processing effort is required. Relevance Theory has two fundamental principles. The first, or the cognitive principle of relevance, states that "human cognition tends to be geared to the maximization of relevance." The second, or the communicative principle of relevance, states that "every act of ostensive communication communicates a presumption of its own optimal relevance" (Sperber & Wilson, 1995, p. 260). The first principle of relevance predicts that an individual has an innate tendency to process an input to yield maximum cognitive effect with least possible processing effort. The second principle predicts that as a hearer, an individual automatically expects that the speaker will provide information which yields enough cognitive effect in return for the processing cost.

A relevance-theoretic view of interpretation of the Japanese riddles is based on the second principle. When encountering the Japanese riddles, an individual, who expects that it would provide enough cognitive effect with least possible processing effort, automatically tries to resolve the incongruities between the two seemingly unrelated schemas corresponding to the target and the response words. When the individual is finally given the rationale for connecting the two unrelated concepts at the 4th phase, he is likely to feel "Aha!" At that point, he is satisfied with the interpretation and stops processing it.

Based on this principle, it was predicted that, if the answer to the riddle was finally judged humorous, there would be little relevance-based understanding in the 3rd phase because no cognitive effect was yet achieved at that time point, and the intensity of relevance-based understanding would go up in the 4th phase because enough cognitive effect was finally achieved then to repay the large processing effort spent during the 3rd phase. It was also predicted that, if a riddle was finally judged banal (non-humorous), relevance-based understanding would peak at the 3rd phase since the individual already found a rationale satisfying optimal relevance. Since the riddle was in this case resolved already by the 3rd phase, it was predicted that there would be no further relevance-based understanding in the 4th phase.

The amygdala as a detector of optimal relevance

Previous lesion and neuroimaging studies have shown that the amygdala is involved in an evaluation of motivationally relevant events (Sander, Grafman, & Zalla, 2003; Zald, 2003; Bach et al., 2008). Several studies have demonstrated the key role of the amygdala in negative emotion, but a few studies have suggested a corresponding role for the amygdala in both positive and negative emotion (Hamann & Mao, 2002; Burgdorf & Panksepp, 2006). So, the view of the amygdala as a relevance detector has been proposed (Sander et al., 2003; Zald, 2003), and many neuroimaging studies have supported the hypothesis (Bach et al., 2008; Ousdal et al, 2008; Herbert et al., 2009; Bach et al., 2011). In this article, we take the hypothesis a step further and propose that the amygdala extends its function in humans as a relevance detector in ostensive communication. Thus, it was predicted that the amygdala would be activated if relevance-based understanding occurred. It was also predicted that the amygdala would be deactivated if no such relevance-based processing occurred.

Previous neuroimaging humor studies report the activation of subcortical structures including the amygdalae during humor appreciation (Mobbs, Greicius, Adbel-Azim, Menon, & Reiss, 2003; Moran, Wig, Adams, Janata, & Kelley, 2004; Bartolo, Benuzzi, Nocetti, Baraldi, & Nichelli, 2006; Wild, Rodden et al., 2006; Watson, Matthews, & Allman, 2007; Bekinschtein, Davis, Rodd, & Owen, 2011; Kohn, Kellermann, Gur, Schneider, & Habel, 2011). We propose that activation of amygdala in humor appreciation can be interpreted as the result of detecting the optimal relevance in humorous utterances — the "Aha" reaction. Other main common activation areas of these humor studies include the left hemisphere of the cerebral cortex: an area around the left fusiform gyrus or the left temporo-occipital junction (Brodmann's area [BA] 37)) to detect incongruity in humorous utterances (Mobbs et al., 2003); the left posterior middle temporal gyrus (BA 21) for semantic comprehension of humor (Moran et al., 2004); the left inferior frontal gyrus including Broca's area (BA 44/45) to resolve the incongruity or ambiguity in humorous utterances (Mobbs et al., 2003; Moran et al., 2004; Bekinschtein et al., 2011); and the medial frontal cortex (Goel & Dolan, 2001; Mobbs et al., 2003; Kohn et al., 2011).

In this study, we used the fMRI method to investigate the relationship between humor appreciation and its time course that composed two factors: the presence/absence of humor (humorous vs. non-humorous) and the expecting/shown rationale (the 3rd phase vs. the 4th phase). We predicted that when a participant explicitly judged the answer to the riddle humorous at the end, its relevance would be detected implicitly at the 4th phase. In addition, it was predicted that when the participant judged the answer to the riddle non-humorous at the end because it was banal, its relevance would be detected earlier at the 3rd phase.

Methods

Participants

Twenty participants (10 females and 10 males; mean age, 23.3 years; range, 18–37 years) were recruited as paid volunteers for the fMRI experiment. All participants had normal/corrected-to-normal visual acuity, and were right-handed according to the Edinburgh handedness inventory (Oldfield, 1971), and no history of neurological/psychiatric illness. They were educated higher than high-school graduates. Written informed consent in order to take part in this study was obtained following procedures approved by the Ethical Committee of the National Institute for Physiological Sciences, Japan.

Preparation of task materials

The riddles had the following structure: “Given A, I'd say B. Do you know why? It is because X.” The topics for the riddles were obtained from an article (Nakamura, 2009) and Internet searches by Google (http://www.google.com) in order to create candidates for strongly humorous riddles. For example, “Given ‘savings,’ I’d say ‘a smile of my wife,’ Do you know why? It is because if they disappear, I will be in trouble.” Then, we altered the response word of each riddle in order to create candidates for weakly humorous version. For example, “Given ‘savings,’ I’d say ‘a credit card,’ Do you know why? It is because if they disappear, I will be in trouble.”

In order to select well-controlled pairs of riddles, 8 normal volunteers (4 females and 4 males; mean age, 27.0 years; range, 22–44 years) participated in a pilot study. We selected a paired riddle if one of the pair was evaluated humorous by over one third of participants and the other one was evaluated non-humorous by over one third of participants. We obtained 24 topics from the article and created 24 pairs of riddles, but 8 were removed after the pilot study. We also obtained 20 topics from the Internet searches and created 20 pairs of riddles, but 2 were rejected. So, finally, we selected 34 pairs of riddles and used them in the fMRI session.

fMRI procedures

Prior to the fMRI session, the participants received detailed instructions and an explanation of the task procedure, and were trained with training stimuli that were 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. Using a liquid crystal display (LCD) projector, the visual stimuli were projected onto a half-transparent viewing screen located behind the head coil of the magnetic resonance imaging (MRI) scanner. Participants viewed the stimuli via a mirror attached to the head coil. The sentence stimuli were written in Japanese and presented with white letters on a black background. The maximum visual angle was 7.8° (horizontal) × 0.9° (vertical).

In each trial, the 1st phase was presented on the screen for 1.5 sec followed by a cross-hair for 1.25 sec, then the 2nd phase appeared for 2 sec followed by a cross-hair for 1.25 sec, then the 3rd phase appeared for 0.75 sec followed by a cross-hair for 1.75 sec, after that the 4th phase was presented for 3.5 sec followed by a cross-hair for 2 sec. The length of each phase was adjusted corresponding to the max length of presented stimuli because timing control was important for the Japanese riddles, yet the length of the 3rd phase was shortened and the time between the 3rd and the 4th phase was lengthened because of reducing the value of correlation coefficients of regressors in imaging data analyses. Then the participant was required to judge whether or not the riddle is humorous and to press the button after the question mark “?”, which was presented for 1 sec followed by a cross-hair for 5 sec, was presented.

We used an event-related design to minimize habituation and learning effects. The 34 paired riddles were presented in a pseudorandom order. The paired riddles were presented in different sessions. In total, two sessions, each with 17 candidates of humorous riddles and 17 candidates of non-humorous riddles, were run, and the session order was counterbalanced across participants.

All images were acquired using a 3-Tesla MR scanner (Allegra; Siemens, Erlangen, Germany). For functional imaging during the sessions, an ascending T2*-weighted gradient-echo echo-planar imaging (EPI) procedure was used to produce 34 continuous 4-mm thick transaxial slices covering the entire cerebrum and cerebellum (time repetition [TR], 2000 ms; time echo [TE], 30 ms; flip angle, 85°; field of view [FoV], 192 mm; 64 × 64 matrix; voxel dimensions, 3.0 × 3.0 × 4.0 mm). Oblique scanning was used to exclude the eyeballs from the images. Each session consisted of a continuous series of 354 volume acquisitions with a total duration of 11 min 48 sec. For anatomical imaging, T1-weighted magnetization-prepared rapid-acquisition gradient-echo (MP-RAGE) images were also obtained (TR, 2500 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).

After the fMRI session, the participant was asked to select the best reason for the judgment among the given possibilities (Nakamura, 2009) in order to remove the reasons in which we were not interested. The given options for judging non-humorous were “non-understandable,” “banal,” “objectionable” and “too serious.” The given options for judging humorous were “sympathetic,” “convincing,” “to-the-point” and “close to banal.” The total duration of the experiment was under 60 min, including the acquisition of the structural MR images and these responses.

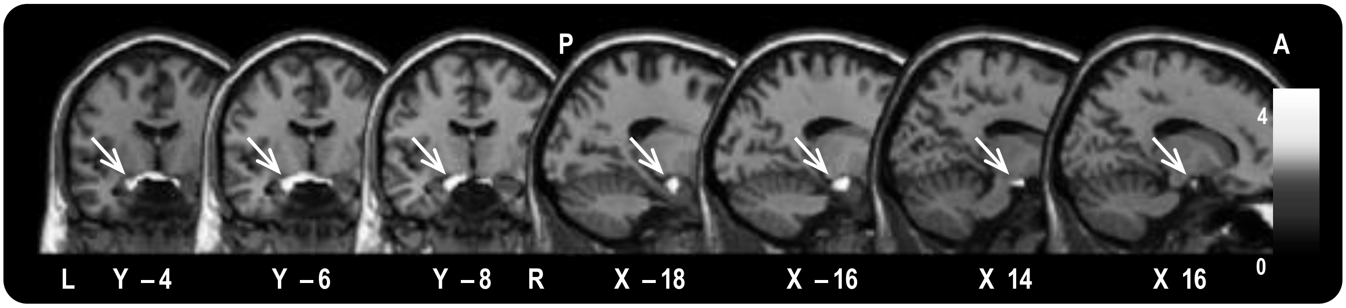

Figure 1: The amygdala as a detector of optimal relevance (an interaction area of the 2 × 2 factorial design).

Data analysis

Performance In this study, we assumed that the judgment about whether or not a riddle is humorous was based on several different reasons, which we separated out using our experimental design. We created paired riddles which contained humorous version and non-humorous version, and we called convincing-banal pairs if one of the pair was judged humorous because it was convincing by a participant and the other of the pair was judged non-humorous because it was banal by the same participant. Only riddles of convincing-banal pairs were included in the following analyses. Other reasons were rejected because they could contain negative values or ambiguous meanings.

Imaging data The preprocessing of the imaging data was performed as follows. The first 6 EPI volumes of each session were eliminated to allow for the stabilization of the magnetization, and the remaining 348 EPI volumes per session (a total of 696 EPI volumes per participant for two sessions) were used for the analyses. The data were analyzed using Statistical Parametric Mapping 8 (SPM8; Wellcome Department of Imaging Neuroscience, London, UK; Friston, Ashburner, Kiebel, Nichols, & Penny, 2007). The EPI volumes were realigned to correct for head motion, and corrected for differences in slice timing within each volume. Then, the whole-head MP-RAGE image volume was coregistered with the mean image volume of the EPI volumes, and segmented into the gray and the white matter volumes using the Montreal Neurological Institute T1 image template. The normalizing parameters of the segmentation were applied to the all EPI volumes. After that, the EPI volumes were spatially smoothed in three dimensions using an 8 mm full-width half-maximum Gaussian kernel.

The signal time course for each participant was modeled with a general linear model. Regressors of interest (trial effects) of the 10 conditions (12e, 3e, 4e, 12a, 3a, 4a, 12z, 3z, 4z, and J) were generated using a box-car function convolved with a hemodynamic-response function (Abbreviation: 12, the 1st and the 2nd phase; 3, the 3rd phase; 4, the 4th phase; J, the judgment phase; e, judging humorous (i.e., convincing of convincing-banal pairs); a, judging non-humorous (i.e., banal of the pairs); z, judging as other six reasons in which we were not interested).

The weighted sum of the parameter estimates in the individual analyses constituted the contrast images, which were used for the group analysis with a random effects-model to make population-level inferences regarding the task-related activation. The contrast images obtained by the individual analyses represent the normalized task-related increment of the MR signal of each participant. In total, the data from 15 participants (other 5 contained no convincing-banal pairs) and four different contrasts (3e, 4e, 3a, and 4a) were incorporated into the 2 (humor effect) × 2 (its time course effect) factorial design (Friston et al., 2007). As a result of the factorial design, a significant interaction was found in the bilateral amygdalae, which we defined as regions of interest and used as an explicit mask. In order to show the difference of activated timing of the Amygdala, four different contrasts (3e vs. 3a, 3a vs. 3e, 4e vs. 4a, and 4a vs. 4e) were used in the one-sample t-tests with the explicit mask image. In order to check the activation of each phase, six different contrasts against the rest condition (12e, 3e, 4e, 12a, 3a, and 4a) were used in the one-sample t-tests.

The statistical threshold was set at $p < .05$ with a correction for multiple comparisons at the cluster level.

Results

Behavioral performance

During the fMRI experiment, 734 riddles (54.0%) were judged humorous, while 626 riddles (46.0%) were judged non-humorous. After the fMRI session, 231 riddles (17.0%) were judged convincing, while 243 riddles (17.9%) were judged banal. Then, the 43 paired riddles (6.32%) were judged as convincing-banal pairs, which were used in the following imaging data analysis (a random-effects model).

Group analysis with a random-effects model

In the 2 × 2 factorial design, no significant main effect was found, but a significant interaction was found in the bilateral amygdalae (see Figure 1 for a spread cluster and Table 1 for peak-levels). In the interaction area, the left amygdala was significantly activated in the 4th phase before the riddle was judged humorous and also in the 3rd phase before the riddle was considered banal (non-humorous), while the right amygdala was significantly activated in the 4th phase before the riddle was judged humorous (see Table 2).

Table 1: The amygdala as a detector of optimal relevance (an interaction area of the 2 × 2 factorial design).

Cluster Size	Peak *p*	Z	Coordinates x	y	z	Location
227	.046	4.72	–18	–6	–20	L Amygdala
	.032	4.81	–14	–8	–16	L Amygdala

Table 2: Difference of activated timing of the Amygdala (results of the one-sample t-test in the interaction area).

Cluster *p*	Size	Z	Coordinates x	y	z	Location
humorous vs. banal (non-humorous) in the 4th phase						
< .001	117	4.43	–18	–6	–18	L Amygdala
.014	17	3.79	16	–4	–20	R Amygdala
.041	2	3.21	2	–2	–12	R Hypothalamus
banal (non-humorous) vs. humorous in the 3rd phase						
.001	57	4.01	–14	–8	–16	L Amygdala
.036	4	3.20	6	–6	–16	R Hypothalamus

When the riddle was to be judged humorous in the end, significant activations were found mainly in the left hemisphere of the cerebral cortex: (12e) the bilateral fusiform gyri (BA 37), the bilateral inferior occipital gyri (BA 17–19), the left middle frontal gyrus (BA 9), and the left middle temporal gyrus (BA 21); (3e) the left inferior frontal gyrus (BA 47/45); (4e) the left posterior rostral medial frontal cortex (prMFC; BA 8/6), the left inferior frontal gyrus (BA 9/45), the left fusiform gyrus (BA 37), and the left inferior occipital gyrus (BA 18/19). When the riddle was to be judged banal (non-humorous), on the other hand, significant activations were found mainly in the left hemisphere and left amygdala: (12a) the bilateral inferior occipital gyri (BA 18–19); (3a) the left amygdala; (4a) the left prMFC (BA 8/6) including the left anterior cingulate cortex (BA 32), the left inferior frontal gyrus (BA 9/45), and the bilateral inferior occipital gyri (BA 18/19).

Discussion

Performance

There are clear individual differences in the way humor is appreciated. In this study, we were interested in the amygdala detecting the optimal relevance during humor appreciation, and we used convincing-banal pairs in order to strictly cancel out the effects in which we were not interested. In the 3rd and the 4th phase of a paired riddle, same participants read same stimuli, so only effect of the 2nd phase, which was modeled out in the 2 × 2 factorial design, was remained. Thus, a significance level in the following analysis can be reached with data of only 15 participants.

Neural activation

The present study revealed that the amygdalae are specifically involved in relevance-based understanding, showing that the amygdalae have a key role in appreciating a riddle humorous through the time course of humor appreciation. We were also able to reproduce the other activations recorded in other studies.

Relevance-related activation of amygdala On the basis of a significant interaction in the 2 × 2 factorial design, we argue that the amygdala is a candidate for relevance-based processing. The left amygdala was significantly activated in the 4th phase when the riddle was to be judged as humorous. It was also activated in the 3rd phase when the riddle was to be judged banal (non-humorous). Thus, we claim that the left amygdala functions as a detector of optimal relevance during humor appreciation. The right amygdala was significantly activated only in the 4th phase when the riddle was to be judged humorous, and hence we argue that the right amygdala is a kind of positive value detector.

While previous studies have suggested that the bilateral or the left amygdala activation involves in positive emotion (Bartolo et al., 2006; Bekinschtein et al., 2011; Mobbs et al., 2003; Moran et al., 2004; Watson et al., 2007), our results suggested that the left amygdala activation involves in relevance detection because it was found not only in the 4th phase of judging humorous (i.e., positive emotion) but also in the 3rd phase of judging non-humorous (i.e., non-positive or negative emotion). If same brain parts are activated in both opposite values, the distinction between positive and negative emotion could not be critical feature, but we argue that the common feature of positive and negative emotion, that is, relevance for the organism is more important.

Humor-related activation of left hemisphere Our results also reproduced previous neuroimaging studies of humor appreciation. The activation of the left fusiform gyrus in (12e) and (4e) is interpreted as incongruity detection of humor (Mobbs et al., 2003). The activation of the left middle frontal gyrus in (12e) and the left inferior frontal gyrus in (4e) are interpreted as incongruity or ambiguity resolution of humor (Mobbs et al., 2003; Moran et al., 2004). So, the activation of these areas corresponds to the incongruity resolution a la Suls (1972). The activation of the left middle temporal gyrus in (12e) is interpreted as semantic comprehension of humor (Moran et al., 2004).

Considering that the prMFC has been suggested to represent and update the value of possible future actions such as response selection (Amodio & Frith, 2006), the activation of the left prMFC in (4e) and (4a) is interpreted as being involved in judging whether or not a riddle is humorous. The left inferior frontal gyrus is also activated in both (4e) and (4a), so it might be also involved in the selection. Considering the participants of this study looked at written riddles, the activation of the inferior occipital gyrus is interpreted as seeing effects. So, our results correspond well to previous neuroimaging studies.

Conclusions

Our results highlight the neural substrates for the detection of optimal relevance. When a participant explicitly judges the answer to the riddle humorous, the relevance of the answer has been detected implicitly as the activation of the amygdala at the 4th phase. On the other hand, when the participant judges the answer to the riddle non-humorous because it is banal, its relevance has been detected as the activation of the amygdala earlier at the 3rd phase. Therefore, we argue that the amygdala is a detector of optimal relevance in the process of humor appreciation.

Acknowledgments

This study was partly supported by Scientific Research on Innovative Areas grant #22101007 (H.C.T.) from the Ministry of Education, Culture, Sports, Science, and Technology of Japan (MEXT), and Challenging Exploratory Research grant #23650224 (H.C.T.), Grant-in-Aid for Scientific Research (S) #21220005 (N.S.), (A) #2124013 (H.C.T., N.S.), and (B) #20330136 (T.M., T.N.) from the Japan Society for the Promotion of Science. A part of this study represents the results of the "Development of biomarker candidates for social behavior" and "Integrated research on neuropsychiatric disorders" projects carried out under the Strategic Research Program for Brain Science by MEXT.

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