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Original Article

ORIGINAL ARTICLE

Humor Appreciation Involves Parametric and Synchronized Activity in the Medial Prefrontal Cortex and Hippocampus

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Abstract

Humor perception is a ubiquitous phenomenon in human societies. In theories of humor perception, three factors, non-seriousness, social context, and incongruity, have been implicated in humor. In another theory, however, elaboration and reinterpretation of contexts are considered to play a role in eliciting humor. Although the neural correlates of humor appreciation have been investigated using neuroimaging methods, only a few studies have conducted such experiments under natural conditions. In the present study, two functional magnetic resonance imaging experiments, using a comedy movie as a stimulus, were conducted to investigate the neural correlates of humor under natural conditions. The subjects' brain activity was measured while watching and enjoying a movie. In experiment 1, a parametric analysis showed that the medial prefrontal cortex (MPFC) and hippocampus/amygdala had a positive relationship with the subjective rating of funniness. In experiment 2, intersubject correlation was analyzed to investigate synchronized activity across all participants. Signal synchronization that paralleled increased funniness ratings was observed in the MPFC and hippocampus. Thus, it appears that both parametric and synchronized activity in the MPFC and hippocampus are important during humor appreciation. The present study has revealed the brain regions that are predominantly involved in humor sensation under natural condition.

Key words: amusement, emotion, empathy, frontal pole, movie

Introduction

Humor is a universal aspect of the human experience and being able to enjoy humor seems to be an essential part of what it means to be human (Martin 2007). Psychological approaches have been used to understand the mental processes underlying humor appreciation for many years. In the relevant theories, three fundamental aspects have been implicated as being important: non-seriousness, social context, and incongruity (Martin 2007). Needless to say, non-seriousness and social context are necessary for humor processing, because serious conditions disallow the ability to enjoy humor, and funniness involves the inference of the mental states of others in a social context. However, the validity of the third aspect, incongruity, has been disputed, because it does not fully explain the emotional and social aspects of humor (Wyer and Collins 1992; Martin 2007). As an alternative to incongruity-resolution, another theory posits that initial thoughts and ideas are not totally replaced by new concepts; rather, their value is only diminished. After an initial encoding of context, the changes in the value of the events that result from a reinterpretation of the event can occur. Further elaboration is conducted in response to the reinterpretation of the initial thoughts, which elicit humor sensation (Wyer and Collins 1992).

In this theory, comprehension, reinterpretation, and elaboration are considered as important processes for eliciting humor. Comprehension refers to the encoding of a stimulus event in terms of previously formed concepts or schemata to understand the event in the context of prior knowledge. Reinterpretation involves resolution of incongruity when unexpected statements or behaviors that cannot be interpreted by previous thoughts and knowledge are encountered. Finally, elaboration refers to the conscious generation of inferences about features that are not captured by these initial processes. This theory, rather than a simple incongruity theory, greatly contributes to understanding dynamic aspects of humor elicitation (Wyer and Collins 1992); however, only a few studies have employed this notion from a neuroscientific perspective to date (Chan et al. 2012).

The neural basis of humor processing has been investigated by using several experimental modalities, such as a positron-emission tomography (PET), functional magnetic resonance imaging (fMRI), and lesion studies in human subjects. In these studies, verbal jokes (Shammi and Stuss 1999; Goel and Dolan 2001; Bekinschtein et al. 2011; Chan et al. 2012; Chan et al. 2013; Feng et al. 2014; McGettigan et al. 2015), humorous cartoons (Shammi and Stuss 1999; Gallagher et al. 2000; Mobbs et al. 2003; Azim et al. 2005; Mobbs et al. 2005; Bartolo et al. 2006; Goel and Dolan 2007; Watson et al. 2007; Samson et al. 2008, 2009; Kohn et al. 2011), and videos/movies (Iwase et al. 2002; Moran et al. 2004; Goldin et al. 2005; Hutcherson et al. 2005; Franklin and Adams 2011; Sawahata et al. 2013) have been shown to subjects as stimuli. A review of the functional neuroanatomy of humor has indicated that a large set of cortical and subcortical brain areas are activated (Vrticka et al. 2013). In particular, the cognitive components of humor are associated with activation in language and semantic areas, including the inferior frontal gyrus and the temporal pole, and if the stimuli involve theory-of-mind components, the medial prefrontal cortex (MPFC) and temporo-parietal junction (TPJ) are activated. Because an emotional component is also found to be involved in humor, regions that comprise the amygdala, nucleus accumbens, and ventral striatum are activated.

However, some questions regarding the neural correlates of humor appreciation remain, because few studies have conducted these experiments under natural conditions, in which the subjects enjoy stimuli during the experiment. Second, experiments based on a model of verbal humor appreciation (e.g., incongruent theory) have tended to focus on cognitive, rather than on emotional and social aspects of humor; and therefore, these studies appear to lack ecological validity. To address these issues, we conducted two fMRI experiments that employed a comedy film as stimulus under natural viewing conditions. In experiment 1, a parametric modulation analysis with subjective rating was conducted using a general linear model (GLM), and in experiment 2, an intersubject correlation (ISC) was computed across participants to investigate neural synchronization while watching the movie.

We hypothesized that, if the results of experiment 1 and those of experiment 2 identified overlapping regions, these could be taken as representing critical brain areas involved in humor perception and appreciation. In addition, as a model of humor processing beyond the incongruent theory, elaboration theory is more likely to be the mechanism underlying elicitation of the amusement sensation by the movie stimulus. From several reasons as mentioned above, we speculated that neural networks involved in social brain (e.g., the MPFC and TPJ) and emotion (e.g., amygdala and striatum) would be active during humor processing. In addition, a region related to episodic memory (e.g., hippocampus) would be involved in humor, because items with emotional contents are more memorable than those without (Murty et al. 2010). Finally, the hippocampus could be predominantly active if elaboration and the reinterpretation of the thoughts and ideas elicit a humor sensation, which is the basis of the elaboration theory, because the hippocampus has been implicated in elaboration of autobiographical memory (Addis et al. 2007; Rabin et al. 2010).

Materials and Methods

Experiment 1

Participants

The study was approved by the ethics committee of the Nagoya University, School of Medicine, and all participants provided written informed consent prior to the experiment.

A total of 41 right-handed healthy subjects, native Japanese individuals, participated in the study. They were divided into the Movie group (12 men and nine women, mean age: 21.5 ± 3.9 [SD] years) and the Mosaic group (12 men and eight women, mean age: 21.1 ± 1.7 years). All participants had normal or corrected-to-normal vision, and had never seen the movie before.

Stimuli

For the Movie group, a comedy movie clip “Mr. Bean” (duration: 8 min 9 s) was presented during the scanning, without sound stimulus. The video clip was shown in color and with 1440 × 1080 resolution. The movie content was understandable to native Japanese subjects even when it was shown without any narration or prior explanation. As a control stimulus, a mosaic version of the movie clip was created by dividing the video into 14 (horizontal) × 11 (vertical) rectangles and averaging color content within each rectangle by using commercial software (Adobe, Premiere Pro, CS4, San Jose, CA). This mosaic film (duration: 8 min 9 s) was presented to the Mosaic group during the scanning, again without sound stimulus.

The subjects viewed the films on a monitor through a mirror attached to the head coil of the scanner. An MRI-compatible LCD monitor (Cambridge Research Systems, Rochester, UK) was used for the presentation. The video occupied a visual angle of 14 (horizontal) × 10 (vertical) degrees in the scanner setting. Both the movie and the mosaic video clips were preceded by a 10-s interval with a fixation point.

Experimental Procedure

The subjects in the Movie group watched the movie stimulus and made a subjective rating of funniness on a 4-point scale, ranging from 1 (not funny) to 4 (very funny), during the scanning. Rating was cued every 7 s by the appearance of a small red circle below the movie, lasting for 2 s (inter-stimulus interval: 5 s). Each subject rated the movie 69 times by pressing one of four buttons on an MRI-compatible response box (Current Designs, Inc., Philadelphia, PA), held in their right hand, as rapidly as possible. The timing was chosen empirically because we needed to collect as many events as possible to increase the statistical power for the parametric analysis, under the limitation of the video length (8 min 9 s). The reason for choosing a fixed onset procedure was that randomly jittered onsets may place an additional cognitive demand on the subjects, due to the unpredictability, and subsequently, eliminate the natural viewing condition. The subjects in the Mosaic group watched the mosaic video clip and made a button press in accordance with a number (1, 2, 3, or 4) that was shown, every 7 s, within a small red circle below the movie (duration: 2 s). The order of the numbers was the same as the order of numbers that was most frequently selected in the Movie group at the same time-point.

A number was assigned from the left-most (1) to the right-most (4) button of the response box in a fixed manner across subjects. The subject was instructed about the task before entering the scanner and underwent a brief training session within the scanner before commencing the task. Changes in the mean and SD of the number pressed during viewing the video and of the reaction time (RT) were computed for each group and were compared between the groups using an unpaired t-test (significance threshold: $P < 0.05$). Figure 1 shows the behavioral data for the Movie and Mosaic groups. After the experiment and outside the scanner, the subjects in the Movie group answered a questionnaire consisting of 10 brief questions regarding the contents of the movie (see Appendix for the questionnaire).

fMRI Acquisition

Functional brain images were obtained during the viewing task in an axial-oblique position covering the whole brain with a 3-T MRI scanner (Verio, Siemens, Erlangen, Germany) that was equipped with single-shot echo planar imaging (EPI; repetition time [TR] = 2.5 s, echo time [TE] = 30 ms, flip angle = 80 degrees, 64 × 64 matrix, 39 slices, voxel size = 3 mm × 3 mm × 3.5 mm) that was sensitive to blood oxygen level-dependent (BOLD) contrast. The number of images taken for each subject was 202 (total scan length: 8 min 25 s).

Preprocessing

fMRI data were analyzed with SPM8 software (Wellcome Department of Imaging Neuroscience, London, UK). After discarding the first four images (10 s) of each run, because of unsteady magnetization, the remaining images were subjected to analysis. First, the signal in each slice was temporally realigned to that obtained in the middle slice by using sinc interpolation, and all the images were spatially realigned to the mean image. All of the images were then normalized to the standard Montreal Neurological Institute (MNI) space by using a transformation matrix obtained from the normalization process of the mean image of each participant to the EPI template image. The normalized and resliced images were spatially smoothed with an 8-mm Gaussian kernel. To investigate possible differences in head motion during scanning between the groups, a root mean square (RMS) value of each of the six realignment parameters (three for translation and three for rotation) has been computed and compared by using a two-way ANOVA, with axis (x, y, z) and group as factors (significance threshold: $P < 0.05$).

First-level Analysis

After preprocessing, statistical analysis of the image data obtained for each participant was conducted with a general linear model. At the first-level (a fixed-effect model), the analysis was conducted using a parametric modulation module. Each trial of button pressing was modeled to convolve to a hemodynamic response function. In this model, the numerical values of the button pressed (1, 2, 3, or 4) were modeled parametrically (both first-order and second-order models were included), along with six head movements as regressors. Therefore, the parametric responses entered into the analysis differed between the individual subjects. High-pass filters (128 s) were applied to the time-series data. An autoregressive model was used to estimate the temporal autocorrelation. The signals of images were scaled to a grand mean of 100 overall voxels and volumes within each run. The same analytical procedure was used for both the Movie and Mosaic groups.

Second-Level Analysis

In the second-level analysis for the Movie group, only the contrast images relating to a first-order parametric function were entered into a one-sample t-test (voxel level threshold: P = 0.001, uncorrected), because analysis of the second-order function did not provide any meaningful results. The brain regions where a neural response was positively and parametrically modulated by the amusement rating were investigated in the Movie group. Table 1 lists significant clusters in the Movie group. In the second-level analysis for the Mosaic group, the same analytical procedure was used (one-sample t-test, $P = 0.001$, uncorrected).

Finally, to investigate specific neural correlates of humor perception by excluding possible confounding effects of motor responses and low level visual attention during viewing, the Movie group and the Mosaic group were compared by using a two-sample t-test (voxel level threshold: P = 0.001, uncorrected). Significant clusters where the signal was greater for the Movie group than for the Mosaic group are listed in Table 2. The clusters are superimposed on the SPM8 template brain in Figure 2. In addition, a two-sample t-test, including the mean RT for button press in each subject as a covariate, was performed. For both one-sample and two-sample t-tests at the second-level analysis, the cluster size threshold was set at 10 voxels according to several other fMRI studies of humor processing (Watson et al. 2007; Samson et al. 2008; Bekinschtein et al. 2011; Chan et al. 2012, 2013). The uncorrected P-values of the cluster-level analysis for each cluster are listed in Tables 1 and 2.

To investigate the relationship between hemodynamics and the subjective rating of the movie, parametric responses in the medial part of superior frontal gyrus and left hippocampus (peak coordinates are listed in Table 2) were extracted from the first-level analysis for each subject. Hereafter, we define the MPFC as the medial part of the superior frontal gyrus. The responses were sorted according to the score (1, 2, 3, and 4) and averaged for each score, and finally, the overall mean across the participants in each of the Movie and Mosaic group and the differential response between the groups were computed. These plots are shown in Figure 3.

Experiment 2

Participants

The study was approved by ethics committee of the Nagoya University, School of Medicine, and all participants provided written informed consent prior to the experiment. A total of 15 right-handed healthy subjects, native Japanese individuals, participated in the second experiment in this study (nine men and six women, mean age: 20.6 ± 2.0 years). All participants had normal or corrected-to-normal vision, and had never seen the movie before.

Stimuli

The same comedy movie clip, “Mr. Bean”, was presented during scanning, without sound stimulus. Experimental settings and visual characteristics of the video clip were the same as those used in experiment 1, although the red circle and number that cued the subject to press the button experiment 1 was omitted in experiment 2.

Experimental Procedure

After a brief introduction to the task, the subjects entered the scanner and passively watched the movie. They were told to enjoy the movie, but to keep their head still during the show. During passive viewing of the video, the subject's brain activity was measured by fMRI. After scanning, the subject was instructed on the second task of the funniness rating, which used an MRI-compatible scroll box (Current Designs, Inc., Philadelphia, PA). No scanning occurred during the second task. The subject again watched the video, but this time, a scale bar was shown on the right side of the screen. The scale bar moved upward and downward as the subject scrolled the response box up and down. The scroll box was held in the subject's right hand. Initially, the height of the scale bar was set at the midpoint of the video height (indicated by "50"). When the subject experienced the scene as amusing, they would scroll upward; the bar then moved upward (the maximum was at the highpoint of the video height, indicated by "100"). When they did not find the scene amusing, they would scroll downward (the minimum was at the bottom of the video, as indicated by "0"). The scroll was immediately reflected on the bar height on the screen and the subject could monitor the vertical movement of the bar. Because one subject's scroll data was not available due to a technical problem, his behavioral data was recorded 6 days later. After the experiment and outside the scanner, the subjects answered a questionnaire consisting of 10 brief questions regarding the contents of the movie (see Appendix for the questionnaire).

Behavioral Data Analysis

The funniness rating score was recorded by numerical values ranging from 0 to 100, with one decimal digit. The scores from the start (0 s) to the end (8 min 9 s) of the movie, and the time stamp, were acquired as a time-series. The time resolution for detecting a change in scroll was 16 ms. First, the time-series of the rating scores were divided by 2.5 s (1 TR) intervals. When there was no score recorded in an interval, the same numerical value as the last score recorded in the previous interval was substituted. Such an event could occur because the rating score was not recorded unless the subject adjusted the scroll value, and data was not always available in every 2.5 s interval. Second, the moving average of 5 s (2 TRs) time windows was calculated by averaging the data between 2.5 s before and 2.5 s after a given TR point (e.g., for the 10 s time-point, the data from 7.5 s to 12.5 s were averaged). The moving average score at every 2.5 s (TR) interval was computed for each subject and finally, the data were normalized to a z-value by subtracting the mean and dividing by 1 SD for each subject's data.

The mean and 1 SD of the time-series data of the z-scored ratings are shown in Figure 4, left panel. To compare the similarity of behavioral responses between the experiments, the mean rating in experiment 1 and the z-scored rating in experiment 2 were correlated for the same time-point (Pearson's correlation coefficient, significance threshold: $P < 0.05$). From the data of experiment 2, only the data for the nearest time-point as in experiment 1 were extracted. The absolute difference in time-points between the two experiments was 0.70 s (0.46). These data are plotted in Figure 4, right panel.

fMRI Acquisition

The fMRI data acquisition protocol was the same as that used in experiment 1.

Preprocessing

Preprocessing was the same as that in experiment 1, except that the EPI data were normalized to the MNI template. In experiment 2, the bounding box options of SPM8 were changed as follows [−90, −126, −72; 90, 90, 108] to conform to the defaults used by the intersubject correlation (ISC) toolbox.

Intersubject Correlation Analysis

ISC analysis (Hasson et al. 2004) was performed to identify areas that responded in a similar way across all subjects during passive viewing of a humorous movie. The ISC toolbox (Kauppi et al. 2010; Kauppi et al. 2014) was utilized to calculate a voxel-wise temporal correlation, using Pearson's correlation coefficient, between every pair of subjects across the whole full-band time-series (198 volumes, after deleting the first four volumes). In the resultant average ISC map, the voxel intensities reflect the degree of ISC across all subjects, throughout the experiment. Voxels with high ISC were presumed to be driven by the visual stimuli; therefore, this method does not require any prior knowledge of the expected signal in response to the movie. Thus, it provides an unbiased opportunity to detect reliable response patterns across subjects under a natural condition, such as watching a movie.

To test the statistical significance of the ISC maps, a non-parametric permutation test for the r statistic was conducted by randomly and circularly shifting each subject's time-course, and calculating the r statistic 1,000,000 times. The null distributions of the average correlation at each voxel generated in this way were found to be normally distributed. Therefore, the P-value of each voxel could be computed by fitting the normal distribution on each voxel. Finally, to correct for multiple comparisons, the false discovery procedure, which controls the false discovery rate (FDR), was applied to the data. Although the significance of the ISC was tested at a significant threshold of $q = 0.05$, FDR corrected, according to several fMRI studies that used ISC analysis (Lerner et al. 2011; Nummenmaa et al. 2012), wide regions survived this significance level ($r = 0.08$ or higher). Therefore, a more stringent corrected value of the statistics was used to threshold the ISC map using an FDR correction at $q = 0.001$ ($r = 0.136$ or higher) (Herbec et al. 2015). The areas with significantly synchronized brain activity during viewing of the movie is shown in Supplementary Figure 1 for a presentation purpose.

Time-Window Analysis of fMRI Data

In the second approach, dynamic ISC of brain activity was computed by calculating the average ISC for each acquired EPI, using a 10-sample (25 s) moving average with a 2-sample (5 s) lag. This approach resulted in 95 ISC maps, each reflecting the moment-to-moment degree of intersubject synchronization across all subjects. The time-series data of the mean values of the correlation coefficient were extracted from each of 63 brain regions, as defined by the Harvard–Oxford brain atlas that is implemented in the ISC toolbox. The time-series data of the mean subjective rating of funniness during video viewing, down-sampled to 1 TR, were aligned with the ISC time-series, assuming a hemodynamic delay of 2 TRs (5 s). The rating data were further processed using the same time sequence as in the ISC map; that is, a 10-sample moving average with 2-sample lag. Thus, a 95 (time-points) × 64 (mean rating and ISCs in 63 regions) matrix was created and analyzed by multiple regression analysis in SPSS (ver. 22, IBM Corporation).

Multiple Regression Analysis

Multiple regression analysis was conducted to investigate in which brain regions changes in the ISC predicted changes in subjective rating in a time-series. This was done by entering the mean rating as a dependent variable and the ISCs in 63 brain regions as independent variables into a multiple regression model using the stepwise method (F_{in} =2.8 and F_{out} = 2.7). After an initial analysis using all variables, one variable (Planum temporale) was excluded from the second analysis, because the variable had a variance inflation factor greater than 10, indicating multiple collinearity. The resultant regions, which were included in the model, as well as the partial regression coefficient, *t*-value, and *P*-value are listed in Table 3. The brain regions that were included in the model are superimposed onto the template brain image of the ISC toolbox in Figure 5.

During the time-course of subjective rating, nine peaks and nine nadirs of funniness were identified. The mean and 1 SD of the ISC at the same point as these peaks and nadirs are plotted in Figure 6. ANOVA was applied using regions and conditions (peak and nadir) as factors (significance threshold: $P < 0.05$). Individual paired *t*-tests were conducted for each of the 17 regions (significance threshold: $P < 0.05$, uncorrected for multiple comparisons).

Region-of-Interest Analysis

To investigate the similarity between the results of experiment 1, which used a general linear model, and those of experiment 2, which used model-free analysis, the ISC computed in experiment 2 were extracted from the clusters found in experiment 1. Values of ISC as time-series data were extracted from the region-of-interest (ROI) set at the MNI coordinate found in experiment 1 (Movie vs. Mosaic contrast, Table 2). A spherical ROI (radius = 8 mm) was drawn at the peak coordinates of the left and right hippocampus, caudate nucleus, MPFC, lingual gyrus, middle occipital gyrus, and superior occipital gyrus. The extracted time-series data of ISC was correlated with the time-series data of subjective rating (Pearson's correlation coefficient, significance threshold: $P < 0.05$; Table 4). Because the present study investigated neural correlates of humor sensation, and in particular, in the higher cortical and subcortical areas, the significant correlations obtained in the MPFC and left hippocampus are shown in Figure 7.

Results

Experiment 1

Behavioral Data

In a debriefing after the experiment, all subjects in the Movie group mentioned that they understood the movie contents and enjoyed it very much. In the questionnaire about the movie, all but one subject were perfectly accurate (100% correct), while the remaining subject was 90% accurate. In the Mosaic group, the subjects did not understand the contents of the video clip; however, some of them mentioned, "I saw something moving, which could have been a man".

In the Movie group, the mean of the subjective rating and RT fluctuated over the time-course of the movie as shown in Figure 1*A*. The overall mean (SD) of the rating and the RT were 2.2 (0.5) and 0.94 s (0.21), respectively. There was no significant correlation between the rating score and the RT in individual subjects or at group level (all $P > 0.05$). In the Mosaic group, the subjects pressed the requested button throughout the experiment, as shown in Figure 1*B*. The overall mean of the response and RT were 2.2 (0.0) and 0.66 s (0.15), respectively. An unpaired *t*-test showed that the mean RT was significantly longer for the Movie group than for the Mosaic group (t [39] = 0.5, $P < 0.01$).

fMRI Data

In the Movie group, there was a significant positive relationship between the funniness rating and the BOLD responses in the bilateral amygdala/hippocampus, left MPFC, left caudate nucleus, right temporal pole, and right lingual gyrus, as listed in Table 1. In these regions, the higher the rating, the higher the brain activity. In the Mosaic group, several regions in the posterior part of the brain, i.e., the post central gyrus, precuneus, inferior occipital gyrus, and cerebellum, were positively

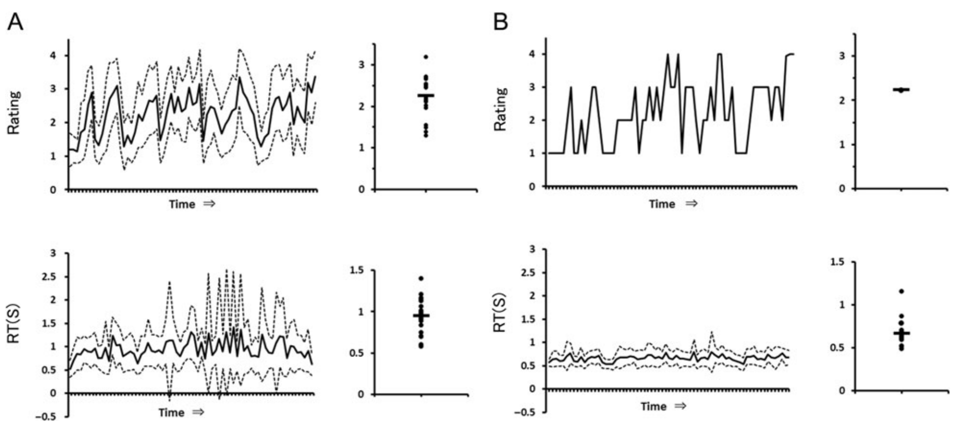

Figure 1. *A*: The behavioral results of the Movie group in experiment 1. The top left panel shows fluctuation in the subjective rating of funniness from the start to the end of a humorous movie. The line indicates the mean, and the dotted lines indicate plus/minus 1 SD of the subjective rating. The top right panel shows the mean rating of each subject throughout the show (a black circle indicates a subject) and the mean rating of all participants (the horizontal bar). The bottom left panel shows the fluctuation of the response time (RT) from the start to the end of the show. The line indicates the mean and the dotted lines indicate plus/minus 1 SD of the RT. The bottom right panel shows the mean RT of each subject throughout the show (a black circle indicates a subject) and the mean RT of all participants (the horizontal bar). *B*: The behavioral results of the Mosaic group in experiment 1. The explanation for each panel is the same as in A. The SD of the rating in the Mosaic group was zero, because all subjects pressed the same button.

Table 1 Significant cluster for Movie group

No.	T	x	y	z	Region	Hemisphere	*k* (voxels)	P[a]
1	6.72	−24	−4	−24	Amygdala/Hippocampus	Lt	222	0.001
2	6.44	12	−72	−8	Lingual gyrus	Rt	456	<0.001
3	5.01	28	12	−28	Temporal pole	Rt	82	0.03
4	4.95	−2	64	8	MPFC	Lt	94	0.021
5	4.56	24	−2	−20	Amygdala	Rt	26	>0.05
6	4.55	−10	0	6	Caudate nucleus	Lt	18	>0.05
7	4.13	18	−16	−14	Hippocampus	Rt	12	>0.05

$P = 0.001$, uncorrected, $k = 10$ voxels, Lt, left; Rt, right; MPFC, medial part of the superior frontal gyrus.
[a]P indicates uncorrected P-value for the cluster size (k).

Table 2 Significant cluster for Movie group versus Mosaic group

No.	T	x	y	z	Region	Hemisphere	*k* (voxels)	P[a]
1	4.97	−20	−12	−20	Hippocampus*	Lt	145	0.009
2	4.81	−4	64	8	MPFC*	Lt	117	0.017
3	4.33	20	−14	−16	Hippocampus*	Rt	68	>0.05
4	4.25	56	−72	10	Middle occipital gyrus	Rt	41	>0.05
5	4.22	20	−94	22	Superior occipital gyrus*	Rt	142	0.01
6	4.04	−10	0	8	Caudate nucleus	Lt	88	0.035
7	3.9	12	−72	−6	Lingual gyrus	Rt	14	>0.05

$P = 0.001$, uncorrected, $k = 10$ voxels, Lt, left; Rt, right. An asterisk indicates the region that remained significant after the mean RT was included as a covariate MPFC, medial part of the superior frontal gyrus.
[a]P indicates uncorrected P-value for the cluster size (k).

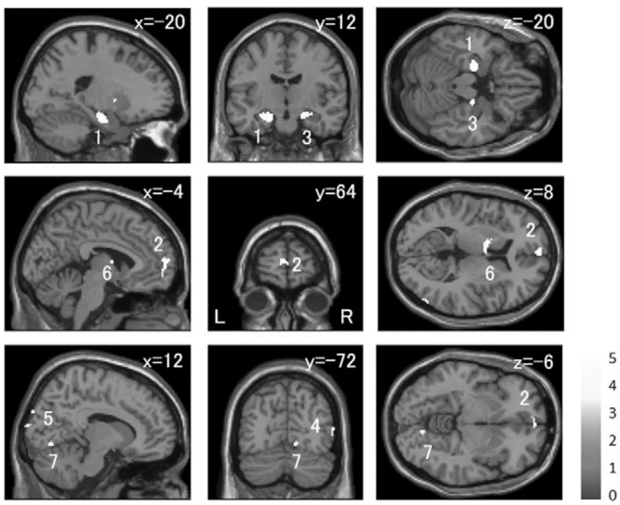

Figure 2. The results of a two-sample *t*-test between the Movie and Mosaic groups are superimposed on the template brain image of SPM8. The significance threshold was set at $P = 0.001$, uncorrected, and $k = 10$ voxels. The coordinates of the *x*, *y*, and *z* axes are shown on each panel. The number in each cluster corresponds to the number in Table 2. The detailed information about the clusters is shown in Table 2. L, left; R; right.

associated with the number on the buttons pressed (data not shown).

A two-sample *t*-test for comparing the groups revealed that the Movie group had significantly greater parametric responses in the bilateral hippocampi, MPFC, caudate nucleus, and several regions in the occipital lobe (Table 2 and Fig. 2). In these areas, the BOLD response was positively modulated by the subjective rating of funniness to a greater extent in the Movie group than in the Mosaic group. A two-sample *t*-test including the mean RT of the subject as a covariate showed that the MPFC, left and right hippocampi, and superior occipital gyrus remained significant among the clusters listed in Table 2 (indicated by an asterisk). Two additional clusters in the bilateral superior temporal gyrus (temporal pole regions; *x*, *y*, *z* = −48, 4, −12; 36, 14, −28) emerged as significant clusters in this analysis. There was no significant effect of group in either translation or rotation parameters in the comparison of head movement between the groups (for translation, group effect: $F = 2.52$, $P = 0.12$; group-by-axis effect: $F = 0.52$, $P = 0.60$, for rotation, group effect: $F = 1.83$, $P = 0.18$; group-by-axis effect: $F = 0.08$, $P = 0.92$).

The parametric responses in the MPFC and left hippocampus are plotted in Figure 3. In the MPFC of the Movie group (Fig. 3A, left), the hemodynamic responses were positively modulated by the funniness rating, showing a gradual increase in peak activity from a score of 1 to that of 4, while in the Mosaic group (Fig. 3A, middle) there was no such modulating effect. As shown in the right panel of Figure 3A, the differential response between the Movie and Mosaic groups were strongly and positively modulated by the subjective funniness rating of the movie. A similar, although somewhat different, pattern of positive modulation was observed in the left hippocampus (Fig. 3B).

Experiment 2

Behavioral data

Analysis of scroll rating revealed a fluctuation of subjective funniness during the movie (Fig. 4A). There was a strong positive correlation between the ratings of the first and second experiments ($r = 0.72$, $P < 0.01$, Fig. 4B), indicating that, in both

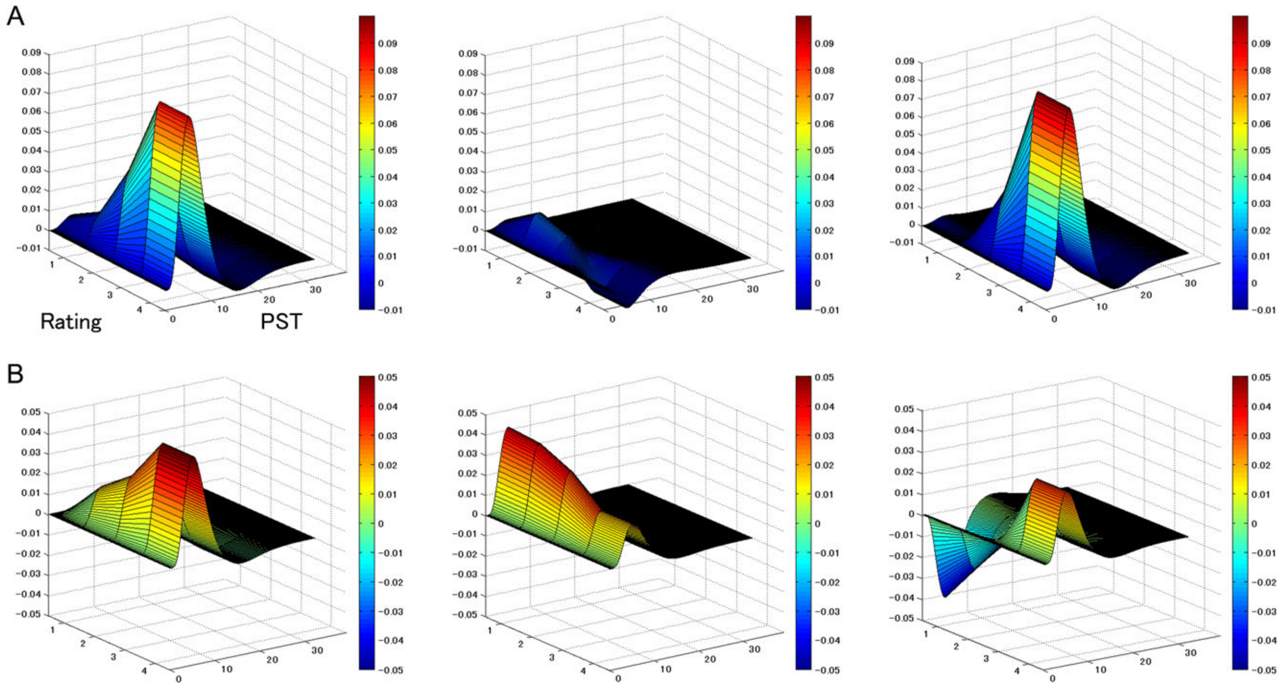

Figure 3. Each three-dimensional figure shows changes in hemodynamic responses according to the subjective funniness rating score for the movie. An x-axis (horizontal) denotes peristimulus time (PST, s) and a y-axis (horizontal) denotes the subjective rating score (1, 2, 3, and 4), while a z-axis denotes the height of the response (arbitrary unit). The color bar indicates the height of the hemodynamic response. The left column shows the responses in the Movie group, the middle column shows the responses in the Mosaic group, and the right column shows the differential responses between the groups. Panel A: the MPFC. Panel B: the left hippocampus. The coordinates of each region are listed in Table 2.

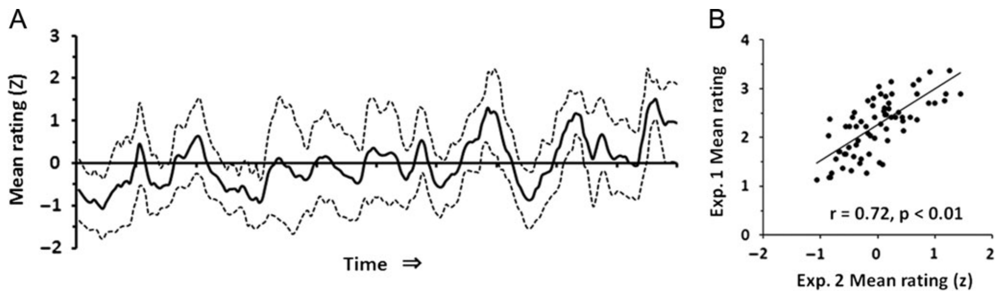

Figure 4. *A*: The behavioral results of experiment 2. The left panel shows a fluctuation in the subjective rating (z score) from the start to the end of a humorous movie. The line indicates the mean and the dotted lines indicate plus/minus 1 SD of the subjective rating score. *B*: A plot of the mean rating at the same time-point in experiment 1 and experiment 2. The regression line, correlation coefficient, and *P*-value are shown.

experiments, subjects had experienced a highly similar sense of amusement during the show. All but one subject were perfectly accurate in answering questions about the movie in the questionnaire, and the remaining subject was 90% accurate.

ISC Analysis of fMRI Data

When using a significance level of $q = 0.001$, FDR corrected, (equivalent to a threshold of $r = 0.136$) widespread regions in the prefrontal, parietal, and temporo-occipital regions had a significant ISC. The distribution of these areas is shown in Supplementary Figure 1 for a purpose of presentation.

Time-Window Analysis and Multiple Regression Analysis

The results of stepwise multiple regression analysis on time-window data revealed that 17 among the 63 brain regions in the whole brain were included in the model (F [17, 77] = 23.8, $P < 0.001$), as shown in Table 3 and Figure 5. Among these regions, the frontal pole, left hippocampus, right hippocampus, and lingual gyrus were significantly different between the Movie and Mosaic groups in experiment 1. The mean correlation coefficient in the 17 brain regions computed for the peak and nadir of the subjective ratings are shown in Figure 6. ANOVA revealed a significant main effect of condition (peak vs. anti-peak, F (1, 272) = 21.24, $P < 0.01$) and region (F (16, 272) = 10.73, $P < 0.01$); however, there was no region-by-condition interaction effect (F (16, 272) = 0.29, n.s.). Individual paired t-tests conducted for each region showed that there was a significant ($P < 0.05$) difference in the mean ISC between the peak and nadir condition in the frontal pole, supramarginal gyrus, and angular gyrus.

Region-of-Interest Analysis of fMRI Data

Among the seven regions that were found significant in the experiment 1, four regions showed a significant positive correlation between the ISC and the subjective rating scale in experiment 2. These were the superior frontal gyrus, lingual gyrus,

Table 3 Significant regions where ISC accounts for subjective rating

Region name	Partial regression coefficient	*t*-value	*p*-value	Significance
Frontal pole	0.12	2.643	0.010	**
Insular cortex	0.245	5.38	0.000	**
Superior frontal gyrus	−0.245	−5.383	0.000	**
Inferior temporal gyrus (temporo-occipital part)	−0.103	−2.263	0.026	*
Superior parietal lobule	0.349	7.675	0.000	**
Supramarginal gyrus (posterior division)	0.095	2.093	0.040	*
Angular gyrus	0.079	1.745	0.085	n.s.
Supplementary motor cortex	0.112	2.461	0.016	*
Frontal orbital cortex	−0.146	−3.207	0.002	**
Parahippocampal gyrus (posterior division)	0.142	3.11	0.003	**
Lingual gyrus	0.301	6.606	0.000	**
Occipital fusiform gyrus	−0.149	−3.272	0.002	**
Heschl gyrus	−0.207	−4.542	0.000	**
Supracalcarine cortex	−0.293	−6.443	0.000	**
Left hippocampus	0.169	3.705	0.000	**
Right hippocampus	−0.251	−5.504	0.000	**
Right accumbens	0.11	2.409	0.018	*

*$p < 0.05$, **$p < 0.01$, n.s., not significant.

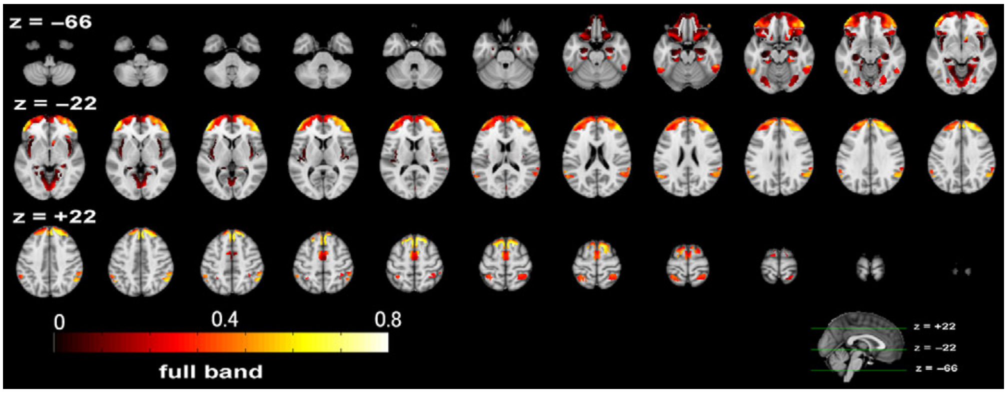

Figure 5. The results of multiple regression analysis are superimposed on the brain atlas of the ISC toolbox. Colored regions are where the time-series of intersubject correlation (ISC) predicted the time-series of the subjective funniness rating of the movie. The detailed information of the cluster is shown in Table 3. The color scale indicates the degree of the correlation coefficient (*r*). "full-band" indicates that the present analysis did not differentiate the frequency band of the signal time-course. The right side of the image represent the right side of the brain.

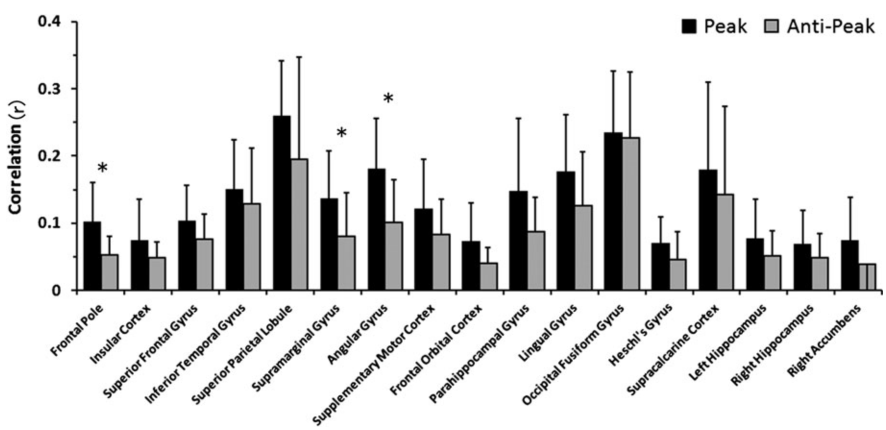

Figure 6. The mean (column) and 1 SD (bar) of the intersubject correlation (ISC) in each brain region listed in Table 3 are shown. The black column indicates the mean ISC at the peak of the subjective funniness rating score, and the gray column indicates the mean at the nadir of the subjective rating score. ANOVA showed that there is a significant difference in the mean ISC between the peak and nadir conditions. For details, see the Results section of Experiment 2. An asterisk indicates statistical significance at $p = 0.05$ in an individual paired *t*-test for each region.

and left and right hippocampus (Table 4). The location of the ROI and the plot for the MPFC and left hippocampus are shown in Figure 7. In these regions, the greater the neuronal synchronization, the higher the subjective rating of funniness.

Discussion

The present study investigated the neural correlates of humor processing by using fMRI during the application of a movie stimulus in normal subjects. In experiment 1, we employed parametric analysis to delineate the brain regions that were positively modulated by the subjective rating of humor, while in experiment 2, we employed an ISC analysis, which is model-free and sensitive to time-varying changes in the emotional response. Experiment 1 revealed that the polar part of the MPFC and hippocampus are positively associated with subjective humor sensation; both these regions survived statistical significance at voxel level (p = 0.001, uncorrected) and cluster-level (p = 0.05, uncorrected) analyses. Experiment 2 showed that synchronized activity in 17 regions of the brain were associated

Table 4 Correlation coefficients between ISC and subjective rating

Region	Hemisphere	correlation coefficient	*p*-value	Significance
Hippocampus	Lt	0.22	0.030	*
MPFC	Lt	0.25	0.013	*
Hippocampus	Rt	0.04	0.680	n.s.
Middle occipital gyrus	Rt	0.31	0.002	**
Superior occipital gyrus	Rt	0.11	0.280	n.s.
Caudate nucleus	Lt	0.13	0.190	n.s.
Lingual gyrus	Rt	0.27	0.008	**

MPFC, medial part of the superior frontal gyrus.
*$p < 0.05$, **$p < 0.01$, n.s., not significant.

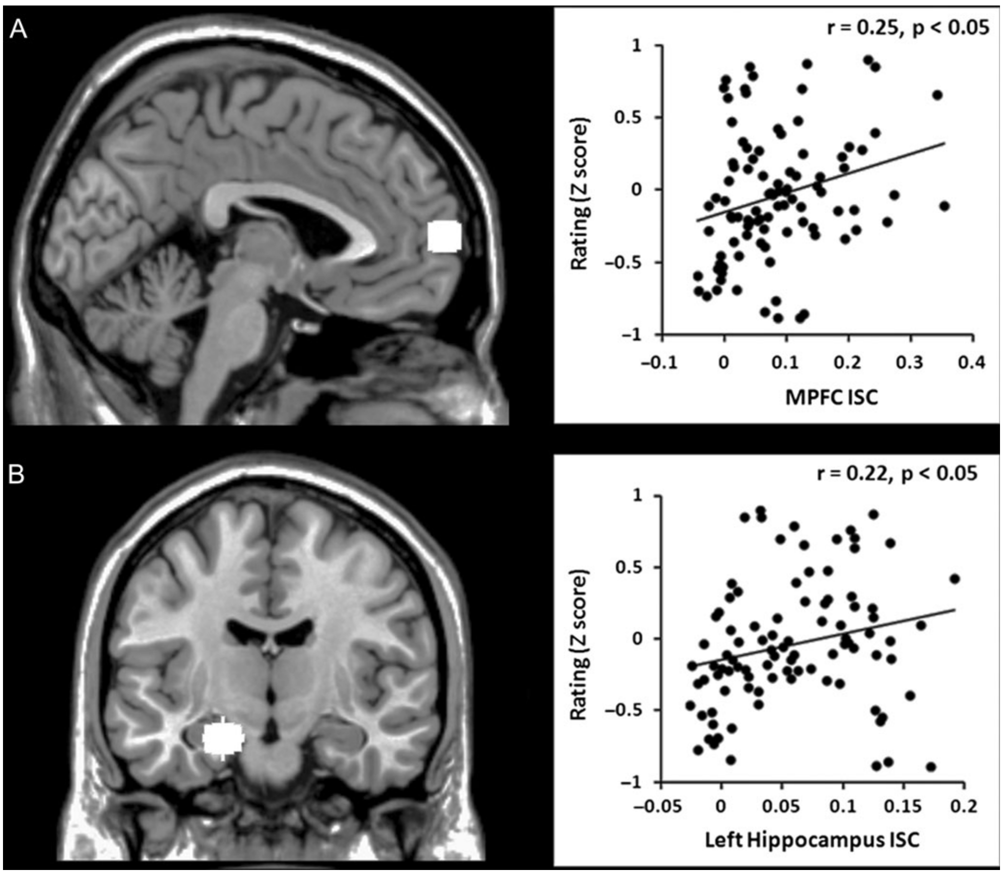

Figure 7. The results of region of interest (ROI) analysis are shown. *A*: A white circle indicates an ROI (spherical, centered at *x*, *y*, *z* = −4, 64, 8, radius = 8 mm) drawn on the MPFC as defined by the Movie vs. Mosaic contrast in experiment 1 (see Table 2). The right panel shows the correlation between the intersubject correlation (ISC; *x*-axis) and subjective funniness rating score (*y*-axis). The regression line, correlation coefficient, and *p*-value are shown in the figure. The higher the ISC in the medial prefrontal cortex (MPFC) region, the higher the subjective rating of funniness. *B*: A white circle indicates an ROI (spherical, centered at *x*, *y*, *z* = −20, −12, −20, radius = 8 mm) drawn on the left hippocampus, as defined by Movie vs. Mosaic contrast in experiment 1 (see Table 2). The right panel shows the correlation between the ISC (*x*-axis) and subjective rating (*y*-axis). The regression line, correlation coefficient, and *p*-value are shown in the figure. The higher the ISC in the left hippocampus, the higher the subjective rating of funniness.

with time-varying changes in humor sensation. In particular, the changes in ISC in the MPFC and hippocampus paralleled changes in the subjective rating of funniness during the show.

As compared with other means of inducing emotion, a movie has the strong advantage of generating intense emotional responses in viewers (Gross and Levenson 1995). Several neuroimaging studies have used movies as experimental stimuli and successfully provoked emotional responses in the subjects during scanning. In a study by Hutcherson et al. (2005), watching a comedy evoked activation in the posterior part of the middle temporal gyrus and insula, whereas watching a sad film evoked activation in the MPFC and amygdala. In a previous fMRI study that used sad and amusing movies as stimuli (Goldin et al. 2005), regression analysis of the happy emotion evoked activation in the MPFC, hippocampus, caudate body, and the posterior part of the superior temporal gyrus; these regions were also found to be significant for the sense of amusement in the present experiment.

In an fMRI study that used amusement films (Franklin and Adams 2011), activation in the bilateral amygdala and TPJ was positively associated with the participants' own rating of humor; these results are consistent with those of the present study. In another study (Moran et al. 2004), activity in the insula and amygdala was involved in humor appreciation, while activity in the posterior part of the middle temporal gyrus and the inferior frontal gyrus was involved in humor detection. Finally, Iwase et al. (2002) showed that viewing a comedy activated the MPFC and the posterior temporal region more than did viewing voluntary face movements. As a whole, these results indicated that the subjective rating of humor sensation is positively related to activity in the MPFC and hippocampus/amygdala region.

Activation of the MPFC and TPJ has also been reported in fMRI studies that used humorous cartoons (Samson et al. 2008; Kohn et al. 2011). Two studies that used cartoons and parametric analysis of subjective humor ratings revealed significant involvement of the MPFC and the TPJ (Goel and Dolan 2007; Watson et al. 2007). The presentation of an incongruity-resolution cartoon (Samson et al. 2009) and a theory-of-mind cartoon/story (Gallagher et al. 2000) has been found to result in activation in the MPFC. The medial temporal lobe was also associated with significant activation of the amygdala and hippocampal regions during processing of humorous cartoons (Mobbs et al. 2003; Bartolo et al. 2006; Wild et al. 2006; Watson et al. 2007).

Humor processing in the brain has been studied using verbal jokes presented with visual and auditory sentences as stimuli. In these studies, the MPFC (Goel and Dolan 2001; Chan et al. 2012), amygdala (Bekinschtein et al. 2011; Chan et al. 2012), and TPJ (Goel and Dolan 2001; Bekinschtein et al. 2011) have been associated with humor perception. In addition, the dorsal part of the MPFC and TPJ have been activated more by point-to-other-type jokes than by point-to-self-type jokes (Feng et al. 2014), indicating that this area is involved in theory-of-mind processes (Koster-Hale and Saxe 2013; Schurz et al. 2014). Finally, a lesion study in humans revealed that patients with right frontal anterior lesions had difficulty in both verbal joke-completion tasks and cartoon-appreciation task (Shammi and Stuss 1999). These results suggest that the frontal lobe, MPFC, and posterior temporal regions are involved in the perception of humor, to various degrees (Wild et al. 2003).

Overall, in these studies, the amygdala is found to be activated frequently as compared with the hippocampus, indicating that they may play distinctive roles in humor processing. The amygdala is more highly activated in funny conditions than in non-funny condition (Mobbs et al. 2003; Bekinschtein et al. 2011; Shibata et al. 2014), and this is positively modulated by the subjective rating of amusement (Bartolo et al. 2006; Franklin and Adams 2011). Moreover, two studies found that the amygdala responses were related with humor appreciation rather than humor detection (Moran et al. 2004; Chan et al. 2012). Accordingly, the amygdala appears to play a key role in the feelings of amusement *per se*, because humor processing is emotionally salient, socially relevant. and biologically valuable for human subjects (Vrticka et al. 2013).

In contrast, activation of the hippocampus is less frequently observed in these studies; a few reports have shown that the hippocampus is related to the subjective rating of amusement (Goldin et al. 2005), and to both visual and verbal humor (Watson et al. 2007). In addition, a correlational analysis revealed that hippocampal activity is modulated by the interaction of funniness and social norms (Goel and Dolan 2007). In experiment 1 of the present study, there was significant involvement of both the amygdala and hippocampus in the Movie group (Table 1), but only the hippocampal activation remained significant when the Mosaic group data were subtracted from the Movie group data (Table 2). These results suggest that the hippocampus may deal with contextual information rather than with visual curiosity during viewing humorous movie.

In experiment 2, which used a natural viewing condition and ISC analysis, wider areas of cortical and subcortical regions showed synchronized activity across participants than seen in experiment 1, which used GLM analysis. In general, there is a notable correspondence between the ISC and GLM approaches, especially in the peaks of synchronized and activated areas; however, the ISC analysis is more liberal than the GLM analysis in a relatively lenient threshold (Pajula et al. 2012). Furthermore, the natural vision paradigm differs markedly from the conventional paradigm, which uses still pictures as a way to reduce several constraints of conventional methods and to approach an ecologically valid condition. Seeing such stimuli usually shows interacting with the context of the movie, and subsequently, a strong emotional response occurs (Hasson et al. 2004). In an early study using ISC analysis, brain areas with across-subject correlation comprised wide areas, including the early as well as the higher-order visual regions in the occipito-temporal and intraparietal cortices (Hasson et al. 2004). The task of experiment 2, in which no overt responses were required, was more natural than the task used in experiment 1 in which subject rated the funniness every 7 s, and greater synchronization was probably induced in experiment 2 than in experiment 1.

However, a high ISC during viewing, as revealed by previous (Hasson et al. 2004) as well as the present studies, is not necessarily related to behavioral and mental processes, such as humor sensation. Therefore, further analyses that associate synchronized activity with behavioral responses is required to understand functional relevance between brain and behavior more comprehensively (Hasson et al. 2008). The present study used multiple regression analysis of the ISC and the degree of humor sensation, and revealed that time-varying changes in the ISC of 17 regions could successfully explain the time-varying changes in humor sensation. Among the 17 regions found to be significant in this analysis, the frontal pole, left hippocampus, and lingual gyrus were the regions in which activation was significantly modulated by the subjective rating of funniness in experiment 1. Thus, a unique finding of the present study is that the results of the model-free ISC approach may parallel the results of the model-based GLM approach, both of which used a natural viewing condition and subjective rating. In addition, the results of the present study fit the elaboration theory rather than the incongruent theory of humor perception and appreciation.

Other anatomical regions where the changes in ISC and humor sensation were positively correlated were the insular cortex, superior parietal lobule, right accumbens, and posterior division of the supramarginal gyrus. The insular cortex (Moran et al. 2004; Hutcherson et al. 2005; Watson et al. 2007) and the nucleus accumbens (Mobbs et al. 2003; Bekinschtein et al. 2011) have been associated with humor appreciation in several neuroimaging studies. The insular cortex and nucleus accumbens have been implicated in visceral sensations associated with emotional awareness (Gu et al. 2013) and the reward/pleasure system (Berridge and Kringelbach 2015), respectively. The posterior division of the supramarginal gyrus is in the vicinity of the TPJ, which has been implicated in humor appreciation in several neuroimaging studies (Iwase et al. 2002; Moran et al. 2004; Goldin et al. 2005; Goel and Dolan 2007; Watson et al. 2007; Franklin and Adams 2011; Kohn et al. 2011; Feng et al. 2014). The TPJ has also been reported to be involved in perspective taking and theory-of-mind processes (Koster-Hale and Saxe 2013; Schurz et al. 2014).

The present study has several important implications for understanding neural correlates of humor processing. First, both experiment 1 and experiment 2 demonstrated that activity in the MPFC, left hippocampus, and right lingual gyrus were closely linked to changes in the subjective perception of funniness. These findings were significant in a parametric modulation analysis of the general linear model as well as in the intersubject correlation analysis. The MPFC has been linked to mental processes, including theory-of-mind, mentalizing, and empathy, and is, more broadly, considered to be a part of the social brain (Frith and Frith 2012) and default mode network (Andrews-Hanna et al. 2010). Therefore, increased signal intensity or synchronization in the MPFC is likely to be associated with increased mentalizing processes and involvement in the social context, which leads to greater amusement perception.

Second, in the present study, the hippocampus, which has been implicated in episodic and autobiographic memory in humans, was also found to be involved in humor appreciation. A possible explanation is that emotional events, both those with positive and those with negative valence, are more memorable than emotionally neutral events and induce greater activity in the amygdala/hippocampus (reviewed (Murty et al. 2010). Alternatively, but not exclusive to emotional memory effects on neural activity (Murty et al. 2010), it has been speculated that the memory elaboration that occurs in the hippocampus would be related to humor appreciation. Upon humor elicitation, initial thoughts and contexts that had been encoded in previous parts of the stimuli are partly replaced by new thoughts and contexts. This may cause changes in the value or importance ascribed to a reinterpretation of the event; and therefore, both previously and newly encoded thoughts and contexts can exist simultaneously. Further memory or contextual elaboration may be required in response to the reinterpretation of these ideas when both the initial and changed representations are present within the subject's mind (Wyer and Collins 1992). These notions fit the comprehensive-elaboration theory, rather than the simple incongruity theory. Several neuroimaging studies have shown that elaborative processes in episodic and autographical memory increases neural activity in the human hippocampus (Addis et al. 2007; Rabin et al. 2010). Interestingly, in both studies, the MPFC was found to be involved in the elaboration of memories cued by a noun (Addis et al. 2007) or a picture (Rabin et al. 2010).

The involvement of the lingual gyrus both in parametric and ISC analyses was unpredictable, as the area is thought to be involved in primary visual functions in humans (Wilms et al. 2010). Several studies have investigated the effect of spatial attention on activity in the primary visual cortices using fMRI, and have shown a relationship between increased attention and enhancing BOLD signals in areas V1, V2, and V3 (Martinez et al. 1999; Somers et al. 1999). We speculate that, as the subjective rating of funniness increases, the participant's attention to the movie scene increases; then, both amplitude and synchronization of BOLD signals are enhanced in the present experiments.

There are several caveats that should be addressed in the present study. In experiment 1, a subjective rating during watching the movie occurred every 7 s. This fixed timing of onsets and relatively short inter-trial-interval (ITI) may not be sufficient to separate trial-by-trial brain responses. However, two parametric fMRI studies employed relatively short ITI; one study was conducted with a word presentation of 100 ms and a fixed stimulus-onset-asynchrony (SOA) of 2.5 s (Hauk et al. 2008), and another study was conducted with a 3-s face presentation and a 1-s ITI on average (Thomas et al. 2012). In addition, although both experiments 1 and 2 in the present study revealed significant involvement of the MPFC and hippocampus in humor processing, the dissociative roles of these regions have not been fully elucidated. Therefore, future research is needed to reveal the functional role of each region.

In conclusion, the present study investigated the neural correlates of humor perception and appreciation using a movie stimulus and two fMRI experiments. Using a novel approach that used intersubject correlation analysis, we found that synchronized activity in the MPFC and hippocampus was correlated with the subjective perception of the degree of funniness. The involvement of the MPFC may imply that empathic concern for actors and scenes, as well as encoding of the social context of the movie, are particularly associated with humor appreciation. The findings of hippocampal activation and signal synchronization during humor appreciation may suggest that elaboration of previously and newly encoded thoughts and contexts that coexist upon humor elicitation induces activity in the medial temporal lobe.

Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/.

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Notes

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Appendix

Ten questions regarding the contents of movie

1. Where did Mr. Bean visit?
   office hospital
2. What vehicle did Mr. Bean follow in his car?
   ambulance fire-engine
3. Who were waiting at the reception before Mr. Bean?
   old couple mother and daughter
4. Who was sitting at the left side of Mr. Bean?
   old person person with bandage
5. What was put on Mr. Bean's left hand?
   kettle vase
6. What was put on a boy's head?
   dish pot
7. After waiting so long, Mr. Bean….?….the board.
   broke inverted
8. Who were quarreling in the waiting room?
   men women
9. What was put on Mr. Bean's right hand?
   umbrella-stand garbage-can
10. Finally, did Mr. Bean attain his aim?
    yes no

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