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Towards a neural circuit model of verbal humor processing: An fMRI study of the neural substrates of incongruity detection and resolution

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A B S T R A C T

The present study builds on our previous study within the framework of Wyer and Collin's comprehension–elaboration theory of humor processing. In this study, an attempt is made to segregate the neural substrates of incongruity detection and incongruity resolution during the comprehension of verbal jokes. Although a number of fMRI studies have investigated the incongruity-resolution process, the differential neurological substrates of comprehension are still not fully understood. The present study utilized an event-related fMRI design incorporating three conditions (unfunny, nonsensical and funny) to examine distinct brain regions associated with the detection and resolution of incongruities. Stimuli in the unfunny condition contained no incongruities; stimuli in the nonsensical condition contained irresolvable incongruities; and stimuli in the funny condition contained resolvable incongruities. The results showed that the detection of incongruities was associated with greater activation in the right middle temporal gyrus and right medial frontal gyrus, and the resolution of incongruities with greater activation in the left superior frontal gyrus and left inferior parietal lobule. Further analysis based on participants' rating scores provided converging results. Our findings suggest a three-stage neural circuit model of verbal humor processing: incongruity detection and incongruity resolution during humor comprehension and inducement of the feeling of amusement during humor elaboration.

Introduction

Humor is unique to mankind and plays an important role in social settings. However, the neurological mechanisms underlying humor comprehension are still not fully understood. In recent years, new technologies have made it possible to develop progressively more refined understandings of these mechanisms. The present study seeks to further contribute to their identification through a novel combination of functional magnetic resonance imaging (fMRI) technology, experimental design, and verbal stimuli constructed to distinguish between the key stages through which the brain processes humor.

The present study builds on earlier research making use of the framework provided by Wyer and Collin's comprehension–elaboration theory of humor (Chan et al., 2012; Wyer and Collins, 1992). The comprehension–elaboration theory of humor claims that humor processing can be segregated into two phases, comprehension and elaboration. Comprehension includes both the experience of surprise resulting from encountering unexpected or incongruous information *and* the re-establishment of coherence which results when the unexpected information is reinterpreted using concepts and schemata from a different knowledge domain. The elaboration phase involves cognitive elaboration of the implications of the reinterpreted situation and subsequent inducement of the feeling of amusement.

Our previous study attempted to differentiate the respective brain areas subserving these two phases in the processing of verbal jokes, by comparing three conditions: funny, unfunny, and garden path. In that study, the bilateral inferior frontal gyri and left superior frontal gyrus were found to be associated with humor comprehension, while the cortical region of the left ventromedial prefrontal cortex and the subcortical regions in the bilateral amygdalae and bilateral parahippocampal gyri were found to be responsible for the feeling

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of amusement during the elaboration process (Chan et al., 2012). The present study seeks to further advance our understanding of the comprehension of verbal humor, by distinguishing the neural substrates of incongruity detection and incongruity resolution. It is expected that our findings will advance our understanding of the neurological mechanisms underlying humor processing and further specify a neural circuit model of verbal humor processing involving three stages: incongruity detection, incongruity resolution, and elaboration.

While a great deal of the humor that we experience on a daily basis is verbal in nature, many studies using fMRI to study humor processing have focused on non-verbal processing, for example, using nonverbal visual cartoons (Azim et al., 2005; Bartolo et al., 2006; Moran et al., 2004; Samson et al., 2008, 2009; Wild et al., 2006) or humorous videos (Moran et al., 2004; Neely et al., 2012). This study joins earlier studies (Bekinschtein et al., 2011; Goel and Dolan, 2001; Ozawa et al., 2000; Uekermann et al., 2006; Watson et al., 2007) in focusing on verbal humor processing.

Within the comprehension–elaboration framework, comprehension can be further divided into two stages, incongruity detection and incongruity resolution (Suls, 1972). For humor to be comprehended as such, it must first be surprising in some way; that is, some incongruity with the preceding context must be *detected*. Then, coherence must be restored or, in other words, the incongruity must be *resolved*. This can be illustrated through consideration of the traditional structure of a joke, which includes a setup and a punch line. The setup is a short statement providing the details necessary to follow the joke, establishing a context which enables expectations to be formed concerning what is likely to follow. The punch line then generates humor by introducing an unexpected 'twist' which in some way violates the expectations established by the setup (Attardo, 1997; Vaid et al., 2003; Wild et al., 2006). In processing the joke, the reader thus must first respond to the setup by establishing a set of expectations, then upon reading the punch line must *detect* an incongruity between the punch line and the setup, and then *resolve* this incongruity in a playful manner.

A growing number of studies have made use of fMRI technology to isolate and identify different neural regions involved in humor processing and a progressively more precise and detailed account of the brain mechanisms underlying humor appreciation has emerged (e.g., Bartolo et al., 2006; Bekinschtein et al., 2011; Goel and Dolan, 2001; Moran et al., 2004; Neely et al., 2012; Wild et al., 2006). As noted, most previous fMRI studies of humor have focused on non-verbal humor, with only a relatively small number focusing on the processing of verbal humor (Bekinschtein et al., 2011; Goel and Dolan, 2001; Ozawa et al., 2000; Uekermann et al., 2006; Watson et al., 2007). One suggestion to emerge from these studies is that the left inferior parietal lobule (IPL) may be active in the semantic processing of verbal humor (Ozawa et al., 2000).

Most previous fMRI studies of humor have used a funny condition and an unfunny (non-funny) condition as stimuli (Azim et al., 2005; Bartolo et al., 2006; Bekinschtein et al., 2011; Goel and Dolan, 2001; Mobbs et al., 2003; Watson et al., 2007; Wild et al., 2006). It appears that the inferior frontal gyrus (Azim et al., 2005; Bartolo et al., 2006; Bekinschtein et al., 2011; Goel and Dolan, 2001; Mobbs et al., 2003; Watson et al., 2007), middle temporal gyrus (Bartolo et al., 2006; Moran et al., 2004), and superior frontal gyrus (Bekinschtein et al., 2011) are associated with the humor comprehension process. However, designs limited to comparisons of funny and unfunny conditions have not been able to fully differentiate the neural substrates involved in the incongruity detection and resolution stages of comprehension processing.

The present attempt locates itself within a series of studies which have sought to distinguish between the different aspects of comprehension processing. Brownell et al. (1983) administered a joke-completion task to 12 patients with right-hemisphere damage (RHD) and 12 matched normal controls. Their participants read the setups to a series of 16 jokes and were asked to choose the best punch lines from a set of four alternatives, which included the funny ending (requiring incongruity detection and resolution), a nonsequitur ending (incongruity detection without resolution), a straightforward neutral ending and a straightforward sad ending (no incongruities to detect and resolve). RHD patients were *less* likely to choose the correct funny ending and *more* likely to endorse the nonsequitur endings. The present study is similar in that it also includes funny, nonsensical ('nonsequitur') and unfunny ('straightforward') conditions; however, it differs in that all participants were neurologically normal volunteers instead of patients.

In Bekinschtein et al. (2011)'s fMRI study, 18 participants listened to 23 each of ambiguous jokes (puns), ambiguous sentences (containing a key word with dual meanings), unambiguous jokes and unambiguous sentences. The processing of stimuli containing ambiguous words (presumably involving the detection and resolution of an incongruity for at least one of the meanings of the words) activated the left interior temporal gyrus (ITG); for the ambiguous *jokes*, the left IFG, right upper MTG, and left SFG were also activated in a whole-brain analysis. The interaction between ambiguity and jokes revealed a significant activation in the left anterior IFG, spreading to the middle frontal gyrus (MFG). As with their study, the present study seeks to refine our understanding of the how ambiguities are processed using verbal stimuli. It contains an additional 'nonsensical' condition, introduced in order to differentiate incongruity detection from incongruity resolution.

Samson et al. (2008) used funny cartoons and nonsense cartoons (cartoons containing an irresolvable incongruity). They found activation in the bilateral supramarginal gyri during successful incongruity resolution, with activity in the right middle frontal gyrus (rMFG) in instances where an incongruity was detected but not resolved. The present study differs from these and other similar attempts (Marinkovic et al., 2011; Samson et al., 2009) to identify the neural bases of incongruity detection and resolution during humor comprehension by making pairwise comparisons using carefully matched funny, unfunny, and nonsensical verbal stimuli. Stimuli in the nonsensical condition contain incongruities which are irresolvable and carefully matched with the other two conditions, in order to better isolate the distinct substrates associated with incongruity detection and resolution.

To summarize, the present study seeks to further specify a three-stage neural circuit model of verbal humor processing, which includes incongruity detection, incongruity resolution and elaboration. It employs an event-related fMRI experiment to identify the neural substrates associated with the detection and resolution of incongruities during the comprehension of the humor in verbal jokes by comparing three carefully paired conditions: unfunny (non-funny or congruous; the baseline condition), nonsensical (irresolvably incongruous) and funny (resolvably incongruous; i.e., humorous). For the verbal stimuli in the unfunny condition, there is no incongruity between the setup and punch line that needs to be detected and resolved. Therefore, no surprise or amusement is expected in this condition. In the nonsensical condition, the punch lines are incongruous and puzzling, but there is no resolution, as there is no logical connection between the setups and punch lines (Shultz, 1974). Compared to the unfunny condition, the nonsensical condition contains an additional, incongruous element and should thus elicit the cognitive operations needed to *detect* this incongruity. Based on earlier findings of involvement of the right medial temporal gyrus in the detection of semantic violations (Kuperberg et al., 2000; Newman et al., 2001; Ni et al., 2000), and of the right MFG in humor processing (Azim et al., 2005; Samson et al., 2008) and context monitoring (Hampshire et al., 2009; Petrides, 2005), we predict that these regions will be involved in the incongruity detection process.

Finally, the funny condition contains a resolvable incongruity. In addition to the operations required to detect the incongruity, it should also call forth those required to successfully *resolve* the incongruity and, thereby, to comprehend the humor (Fig. 1). Our earlier study (Chan et al., 2012) found activation of the bilateral IFG during humor comprehension; other research has found greater activation in the left IFG (Bekinschtein et al., 2011; Rodd et al., 2005; Samson et al., 2008) and right IFG (Moran et al., 2004) related to the resolution process. Similarly, our earlier study found activation of the left SFG during humor comprehension, and other research on humor processing has associated this area with incongruity resolution (Bekinschtein et al., 2011). Finally, the left inferior parietal lobe has been associated with semantic integration and coherence (Chou et al., 2006, 2009). We therefore predict that these regions (bilateral IFG, left SFG and left IPL) will be associated with incongruity resolution. This successful resolution completes the comprehension stage and leads on to the elaboration stage (Fig. 2). In the present study, the setups were the same across all three conditions, with only the punch lines varying, so that the observations should reflect the new information in the punch line with the schemata pre-activated by the setup.

The present study thus made use of a different design in an attempt to differentiate the respective brain areas corresponding to humor comprehension in the processing of verbal jokes, by comparing three conditions: funny, unfunny, and nonsensical. Based on the comprehension–elaboration framework (Wyer and Collins, 1992), incongruity-resolution theory (Suls, 1972), and the finding of previous neuroimaging studies of humor processing, we hypothesized that (non-humorous) nonsensical stimuli, in comparison with the unfunny stimuli, would elicit increased activation related to incongruity detection in several brain regions, including the right middle temporal gyrus and right medial frontal gyrus. We also predicted that the funny stimuli, in comparison with the nonsensical stimuli, would elicit increased activation related to resolution of incongruity in several brain regions, including the bilateral inferior frontal gyrus, left superior frontal gyrus and left inferior parietal lobule.

Material and methods

Participants

Twenty two neurologically healthy volunteers [9 males and 13 females aged 20–29 years, 21.86 ± 2.17 years (mean ± SD)] participated in this study. They were all right-handed (as determined by the Edinburgh Handedness Inventory; Oldfield, 1971), native Mandarin speakers. The study was approved by the Research Ethics Committee of the National Taiwan University Hospital, and all of the subjects gave their informed consent to participate before commencing the experiment.

Stimuli

Sixty-four stories in Mandarin Chinese were selected, including sixteen stories for each of three different conditions: funny, unfunny, and nonsensical. Sixteen filler stories were also included. Each story contained two components: the setup and the punch line. The stories were standardized for length and presented in the same pseudorandom order to all participants. The setups were 110–130 characters in length (mean = 126.25) and the punch lines were 15–30 characters in length

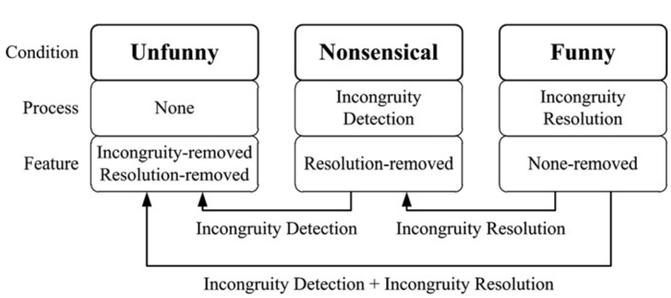

Fig. 1. Cognitive humor processing: segregating incongruity detection and incongruity resolution processing. The unfunny condition is the baseline condition.

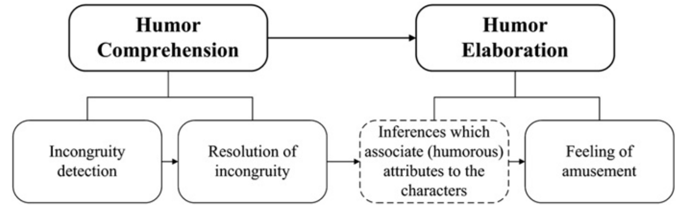

Fig. 2. The comprehension–elaboration theory of humor. Comprehension includes detection and resolution of incongruities, and elaboration includes humor-related inferencing and inducement of the experience of amusement.

(mean = 27.70). The setup and punch line lengths were matched across conditions. The test items were divided into three versions. Each participant received one version. Our presentation was balanced across participants so that a particular story appeared once in each version.

The three conditions were designed to segregate incongruity detection and resolution processing. In the funny jokes, an incongruity was created and then resolved using information from the punch line. For example,

> *Setup:* Peter bought some farmland and started plowing it himself with a tractor. Not long after, he found a front tooth that the tractor had dug up. He felt a bit strange, but kept on plowing. About a hundred meters later, he found another tooth. "Something is definitely wrong," he thought to himself. After just 30 more steps, he found several more teeth. Now he was really frightened. That night he wrote to the previous owner of the land and asked "Was this piece of land ever used as a graveyard?" *Punch line:* Two days later, the old owner replied, "No. Don't worry. It used to be a football field."

To create matching stimuli in the other conditions, stories in the unfunny and nonsensical conditions were created by replacing the punch line in the funny condition. The unfunny condition was generated by replacing punch lines with semantically congruous responses, such as "Two days later, the old owner replied, 'Yes, actually it was a graveyard.'" The nonsensical condition was generated by replacing punch lines with nonsensical sentences designed to result in irresolvable incongruities, like "Two days later, the old owner replied 'Yes, the cliff is now behind you!.'"

Prior to the fMRI experiment, the materials for the experiment were rated by a separate group of 33 native participants (12 males and 21 females, aged 22.06 ± 2.67 years) who received the same standardized instructions. The participants viewed each stimulus on a computer monitor and rated it on its degree of comprehensibility, funniness, and on the 'surprisingness' of the punch line (i.e., the degree to which the stimuli were surprising) using a 9-point Likert scale (ranging from 1 = extremely incomprehensible/unfunny/unsurprising" to 9 = "fully comprehensible/funny/surprising").

Comprehensibility, funniness, and surprisingness rating scores from the pre-test of the stimuli are shown in Table 1. A one-way repeated-measures ANOVA performed on participants' comprehensibility ratings was significant, $F(2, 64) = 226.45$, $p < .001$, with the funny and unfunny conditions being more comprehensible than the nonsensical condition. There was no significant difference in the degree of comprehensibility between the funny and unfunny conditions. A one-way repeated-measures ANOVA on participants' funniness ratings was also significant, $F(2, 64) = 395.98$, $p < .001$, with the funny condition having higher funniness scores than the other two conditions. Finally, a one-way repeated-measures ANOVA on participants' surprisingness ratings was significant, $F(2, 64) = 49.59$, $p < .001$, with the funny and nonsensical stimuli being rated as more surprising than were the unfunny stories.

Reaction times were also collected for each setup and each punch line, with participants asked to press the space key as soon as they understood the content. For the setup, reaction times for the three

Table 1
Comprehensibility, funniness and surprisingness ratings from the pre-test of the stimuli.

Condition	Comprehensibility ratings		Funniness ratings		Surprisingness ratings	
	Mean	SD	Mean	SD	Mean	SD
Funny	7.71	0.92	5.48	1.20	5.98	1.15
Unfunny	7.55	0.84	1.79	0.72	3.81	1.01
Nonsensical	3.58	1.48	1.59	0.60	6.25	1.27

SD: standard deviation.

conditions were non-significantly different, while for the punch line, reaction times for comprehensibility were significantly faster for the funny and unfunny conditions than for the nonsensical condition.

Experimental paradigm

The present study used an event-related fMRI paradigm. Once in the MRI scanner, participants were first presented with the word "ready." Subsequently, each participant was presented with 64 verbal stories. The average stimulus duration was 39 s with randomly jittered interstimulus intervals (ISI) varying from 5 to 9 s with a mean value of 7 s (Fig. 3). Within a story, the setup was shown for 20 s, followed by the punch line for 9 s. Thereafter, participants were asked to provide a subjective comprehensibility judgment by pressing one of two buttons on a keypad in their hand, lasting for 3 s. Pressing the button beneath the index finger indicated 'comprehensible' and pressing the button beneath the middle finger indicated 'incomprehensible'. The use of hand for the button-press responses was counterbalanced in the scanner. Because the purpose of this study was to examine distinct brain regions associated with the cognitive processes required for detecting and resolving incongruities during humor comprehension, we did not assess funniness ratings in the scanner. There were four functional runs in total. Stimuli in the three experimental and filler conditions were randomly distributed in the four functional runs. There was a 2-min break between each functional run. Each functional run took approximately 10 min and 24 s. The total duration of the experiment for each participant was approximately 48 min and 15 s. Before entering the fMRI scanner, participants were reminded not to move their heads if they laughed.

Image acquisition

Images were acquired on a 3-Tesla scanner (Medspec, Bruker, Ettlingen, Germany) equipped with a bird-cage quadrature head coil at the National Taiwan University. Visual stimuli were presented to the participants via a goggle display system (Resonance Technology, CA, USA). Twenty-six axial slices (4 mm thick with a 1-mm interleaved gap) parallel to the anterior and the posterior commissure (AC–PC) and covering the whole brain were imaged with a temporal resolution of 3 s using a single-shot, T2*-weighted gradient echo-planar images (EPIs) spiral pulse sequence (repetition time (TR) = 3000 ms, echo time (TE) = 33 ms, flip angle = 90°). The field of view (FOV) was 240 × 240 mm^2, and the matrix size was 64 × 64, giving an in-plane spatial resolution of 3.75 mm. Each functional run acquiring 211 volumes took 10 min and 24 s. Data acquired during the first three TRs in each functional run were discarded to avoid T1 equilibrium effects.

Image analysis

Data were analyzed using SPM8 software (Statistical Parametric Mapping, Wellcome Department of Cognitive Neurology, London, UK). The functional images were corrected for differences in slice-acquisition time to the middle volume and were realigned to the first volume in the scanning session using affine transformations. The movement was no more than 3 mm in any plane. Co-registered images were normalized to the standard Montreal Neurological Institute EPI template, and the 3 × 3 × 3-mm voxel size of the written normalized images. Statistical analyses were calculated on data that had been spatially smoothed using an 8-mm full-width-at-half-maximum (FWHM) Gaussian kernel, with a high-pass filter (128-s cutoff period) in order to remove low frequency artifacts.

Data from each participant were entered into a general linear model using an event-related analysis procedure. Stimuli were treated as individual events for analysis and modeled for the punch line using a canonical hemodynamic response function (HRF). Parameter estimates from contrasts of the canonical HRF in single subject models were entered into random-effects analysis using one-sample *t*-tests across all participants to determine whether there was significant activation during a contrast. We compared the nonsensical condition to the unfunny condition, and the funny condition to the nonsensical condition.

According to our prior behavioral experiment, the mean reaction time for the comprehension processing of verbal jokes in a punch line was about 5–6 s. The average reaction time for comprehension processing was 5039.39 ± 2820.57 ms for the funny condition, 5152.39 ± 2712.22 ms for the unfunny condition, and 6529.12 ± 3582.36 ms for the nonsensical condition. Therefore, we concluded that it was possible to use a canonical HRF to estimate the punch lines as events. Additionally, in order to detect the regions activated during the incongruity detection process, we carried out a conjunction analysis (using MarsBaR and WFU PickAtlas in SPM8) of the regions active in both the nonsensical and funny conditions.

In order to test the predictions made in the introduction, a region of interest analysis was performed (Poldrack et al., 2008). Eight hypothesis-driven ROIs, with a radius of 10 mm centered at peak voxels of brain regions, were used. Based on the areas predicted to be associated with incongruity detection, we included the right middle temporal gyrus (rMTG, BA21 in Bekinschtein et al., 2011; Lambon Ralph et al., 2010) and the right medial frontal gyrus (rMFG, BA6/8 in Samson et al., 2008). Based on our predictions for incongruity resolution, we included the left dorsal inferior frontal gyrus (IFG, MNI coordinates [−42, 11, 25], BA9 in Chan et al., 2012), right IFG (MNI coordinates [33, 27, 1], BA47 in Chan et al., 2012), left anterior IFG (MNI coordinates [−54, 35, 13], BA46 in Chan et al., 2012) two ROIs within the left SFG (MNI coordinates [−6, 5, 67], BA6 in Chan et al., 2012; and BA8 in Bekinschtein et al., 2011) and the left inferior

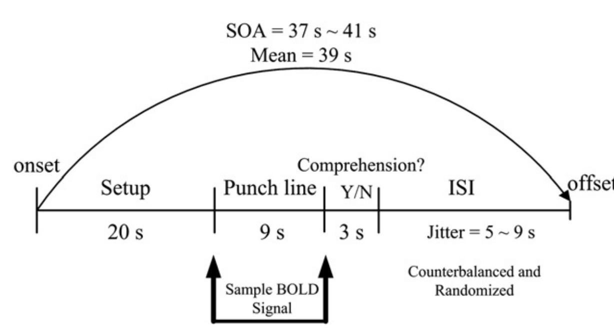

Fig. 3. Stimuli were presented in an event-related fMRI paradigm, with each verbal stimulus being presented randomly. Stimulus-onset asynchrony (SOA) is the amount of time between the start of one stimulus and the start of another stimulus.

parietal lobule (IPL, BA39/40 in Chou et al., 2006, 2009). (MNI coordinates were available for areas taken from Chan et al., 2012.) We then extracted the beta values from peak voxels of brain regions.

To evaluate the brain–behavior relationship, we also performed post-scan ratings on the surprisingness and comprehensibility of each punch line for all participants. Participants were asked to rank each stimulus for its degree of surprisingness and comprehensibility using a 9-point Likert scale. To further investigate incongruity detection, we split the stimuli into the high versus low surprisingness conditions according to the average of their rating scores on surprisingness. 'Surprisingness' refers to the degree to which the stimuli were surprising, unexpected and/or puzzling. Also, to further investigate incongruity resolution, we split the stimuli into high versus low comprehensibility conditions according to the average of their rating scores on comprehensibility. Comprehensibility refers to the degree to which the incongruities present in the stimuli were resolvable. All reported areas of activation were considered significant at $p<.05$ corrected for familywise error rate (FWE) for multiple comparisons at the voxel level with a cluster size greater than or equal to 10 voxels. To visualize the signal change on significant brain regions, time courses were extracted from the beta values of peak voxels of the regions.

Results

Behavioral results

In terms of comprehensibility ratings during the scanning, the mean rating scores for comprehensibility were 93.71% for the funny condition, 89.31% for the unfunny condition, and 8.29% for the nonsensical condition. A one-way repeated-measures ANOVA on participants' rating scores was significant, $F\ (2,\ 42)=948.27$, $p<.001$. Bonferroni post-hoc tests revealed that the funny and unfunny conditions were more comprehensible than the nonsensical condition. There was no significant difference in the degree of comprehensibility between the funny and unfunny conditions.

fMRI results

Incongruity detection: the nonsensical versus unfunny conditions

The contrast of the nonsensical versus unfunny conditions for the ROIs produced greater activation in the right middle temporal gyrus (MTG, BA 21) and right medial frontal gyrus (MFG, BA 6). These results are summarized in Table 2 and Fig. 4.

Incongruity resolution: the funny versus nonsensical conditions

The contrast of the funny versus nonsensical conditions for the ROIs produced greater activation in the left superior frontal gyrus (SFG, BA 8) and left inferior parietal lobule (IPL, BA 40). These results are summarized in Table 2 and Fig. 5.

Incongruity detection: further analysis of surprisingness ratings

Based on the rating scores, the contrast of the high versus low 'surprisingness' conditions for the ROIs produced greater activation in the right MTG (58, −1, −8; BA 21, 69 voxels; $Z=3.13$, $p<.05$ FWE corrected) and right MFG (12, −10, 66; BA 6, 38 voxels; $Z=3.21$, $p<.05$ FWE corrected). The results are consistent with those shown in Table 2 for incongruity detection, providing further support for our account of the neural substrates associated with the detection of incongruities in the humor comprehension process.

Incongruity resolution: further analysis of comprehensibility ratings

Based on the rating scores, the contrast of the high versus low comprehensibility conditions for the ROIs produced greater activation in the left SFG (MNI coordinates: −9, 47, 45; BA 8, 96 voxels; $Z=5.42$, $p<.05$ FWE corrected) and left IPL (−60, −49, 42; BA 40, 56 voxels; $Z=4.97$, $p<.05$ FWE corrected). The results are consistent with those shown in Table 2 for incongruity resolution, providing further support for our account of the neural substrates associated with incongruity resolution in the humor comprehension process.

Conjunction analysis

In order to examine the regions involved in the incongruity detection process, we performed a conjunction analysis (using MarsBaR and WFU PickAtlas in SPM8) of the regions activated in both the nonsensical and funny conditions. The conjunction analysis, masked by the main effect of incongruity detection ($p<.05$ uncorrected, 10 voxels), was performed to highlight the regions of activations associated with nonsensical and funny conditions [conjunction (nonsensical–unfunny), (funny–unfunny)]. This analysis revealed a significant activation in the right middle temporal gyrus (MNI coordinates: 57, 2, −11; BA 21, 56 voxels, $p<.05$ FDR corrected).

Discussion

In the present study, an event-related fMRI experiment was used to identify and distinguish the neural substrates of the incongruity detection and resolution processes during comprehension of verbal jokes. The activations believed to be related to the detection of incongruities were identified by comparing a nonsensical condition with a paired unfunny condition. The results confirm that the right MTG and the right MFG are involved in processing irresolvable incongruities, where there is no re-establishment of a deeper coherence with the preceding context (Goel and Dolan, 2001; Mason and Just, 2007; Moran et al., 2004). In contrast, resolution-related activations were identified in the left SFG and left inferior parietal lobule (IPL) by comparing the funny condition with the paired nonsensical condition.

Starting with the findings for the incongruity detection process, both the ROI-based analysis and further analysis of surprisingness ratings found involvement of the right MTG. This is consistent with

Table 2
Brain activations of eight ROIs for the contrast of the nonsensical versus unfunny conditions (incongruity detection) and for the contrast of the funny versus nonsensical conditions (incongruity resolution).

Side	Region	Nonsensical versus unfunny						Funny versus nonsensical					
		MNI coordinates						MNI coordinates					
		BA	Voxels	x	y	z	Z score	BA	Voxels	x	y	z	Z score
L	Dorsal inferior frontal gyrus	–	–		–		–	–	–		–		–
R	Inferior frontal gyrus	–	–		–		–	–	–		–		–
L	Anterior Inferior frontal gyrus	–	–		–		–	–	–		–		
L	Superior frontal gyrus (BA 6)	–	–		–		–	–	–		–		
R	Middle temporal gyrus	21	78	57	2	−8	4.70	–	–		–		–
R	Medial frontal gyrus	6	66	9	−13	64	3.95	–	–		–		–
L	Superior frontal gyrus (BA 8)	–	–		–		–	8	88	−12	44	46	5.41
L	Inferior parietal lobule	–	–		–		–	40	57	−60	−49	40	5.10

Note: MNI = Montreal Neurological Institute; L = left; R = right; BA = Brodmann's area; Voxels = number of voxels in cluster $p<.05$ FWE (familywise error rate) corrected at the voxel level, only clusters greater than or equal to 10 are presented.

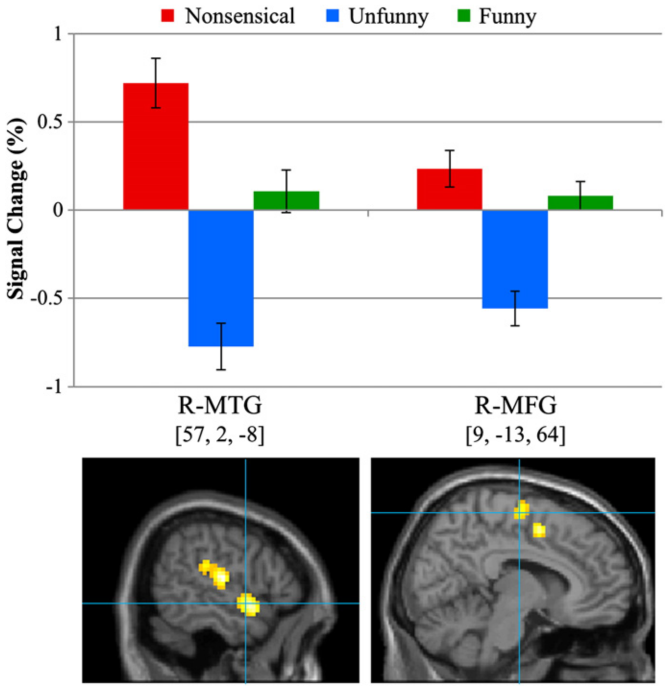

Fig. 4. Incongruity detection. Top: Bars show beta values for 2 regions of interest (ROIs) (peak voxels for each of the three conditions: nonsensical, unfunny, and funny). Bottom: Sagittal brain images for the 2 ROIs. Greater activations were found for the nonsensical versus unfunny conditions in the 2 ROIs, including right middle temporal gyrus (R-MTG) and right medial frontal gyrus (R-MFG).

a number of findings from earlier studies of humor and language processing. Goel and Dolan (2001) found increased activation of the bilateral MTG during joke comprehension, and Moran et al. (2004) found involvement of the right MTG during humor detection. Studies of language processing (not involving humor) have found that the right MTG is involved in the storage of semantic information (Wiggs et al., 1999) and in detecting semantic violations (Kuperberg et al., 2000; Newman et al., 2001; Ni et al., 2000). Furthermore, our findings are consistent with recent accounts of the more general role played by the anterior temporal lobe in terms of semantic memory. Semantic memory (also called conceptual knowledge) is the aspect of human memory that corresponds to general knowledge of objects, word meanings, facts and people (Patterson et al., 2007). Critical components of the network underlying semantic memory are believed to be located in the anterior portion of the temporal lobe. The functions of recognizing and categorizing stimuli may explain the involvement of this region in detecting incongruities (Lambon Ralph et al., 2010).

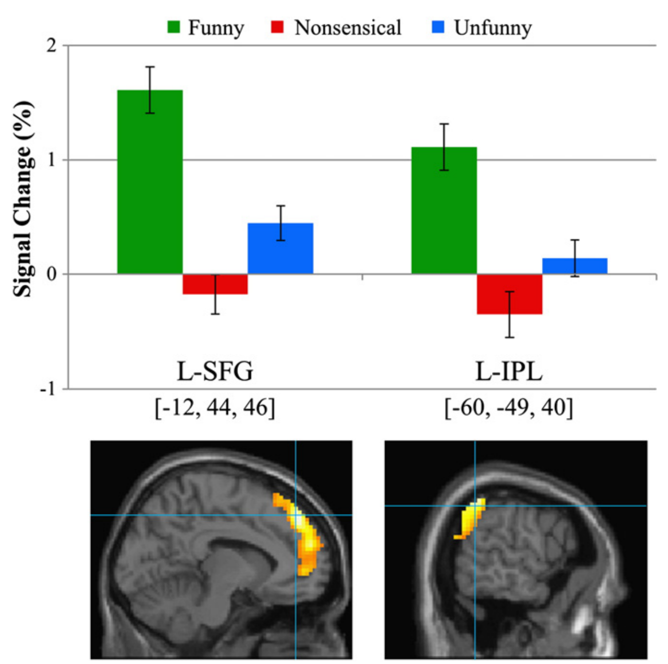

Fig. 5. Incongruity resolution. Top: Bars show beta values for 2 regions of interest (ROIs) (peak voxels for each of the three conditions: funny, nonsensical, and unfunny). Bottom: sagittal brain images for the 2 ROIs. Greater activations were found for the funny versus nonsensical conditions in the 2 ROIs, including left superior frontal gyrus (L-SFG) and left inferior parietal lobule (L-IPL).

In addition to the right anterior middle temporal lobe, the right middle frontal gyrus (rMFG) may be associated with the processing of incongruity detection for language-based humor. This region has been implicated in executive functioning that may be crucial to examining, deconstructing, and attempting to 'get' jokes (Azim et al., 2005; Samson et al., 2008).

Turning to incongruity resolution, the current study found activation in the left SFG and left IPL in contrasts of the funny condition with the paired nonsensical condition. The resolution process seems to involve organizing thoughts, developing insights, disambiguating information, schema-shifting and developing bridging inferences in order to establish a new context (Bekinschtein et al., 2011). Both the left SFG and the left IPL have also been implicated in executive functions. In particular, the SFG may contribute to higher cognitive functions (du Boisgueheneuc et al., 2006; Owen, 2000; Petrides, 2000). The SFG has been found to be more active in the incongruity-resolution condition in other studies (Bekinschtein et al., 2011; Samson et al., 2009). The left SFG may also play a role in the integration of concurrent information in the resolution process of humor comprehension (Buxbaum and Saffran, 2002; Chao and Martin, 2000).

The left IPL may be associated with the capacity to understand causal relationships between the setup and punch lines (Samson et al., 2009). These suggestions are also consistent with a study by Lee et al. (2011), which found stronger semantic association to be correlated with greater activation in the left IPL (BA 40). Activation in this region has also previously been identified in semantic tasks, including associative judgments (Binder et al., 2004), similarity judgments (Price, et al., 1999), and concrete word judgments during semantic tasks (Chee, et al., 2002). In sentence comprehension, the role of the left IPL is to integrate discrete pieces of semantic information into a global meaning (Humphries et al., 2006, 2007). In the present study, it could be that the left IPL was involved in the process of resolving incongruities and creating a new, coherent interpretation linking the setup to the punch line.

Returning to Brownell et al.'s (1983) patient study, the RHD patients were *less* likely to choose the correct funny ending and *more* likely to endorse the nonsequitur endings. The authors concluded that the RHD patients retained the ability to detect surprises (incongruities) but had a diminished ability to successfully re-establish coherence (resolve the incongruities), or, put differently, that the right hemisphere is active in the resolution of incongruities, but not in the detection of incongruities. Their conclusion is consistent with other patient studies (Bihrle, Brownell, Powelson, and Gardner, 1986). Inconsistent with their finding, we found that the detection of incongruities was associated with greater activation in the MTG and MFG in the right hemisphere. Moreover, the resolution of incongruities was associated with greater activation in the SFG and IPL in the left hemisphere. The reason for the discrepancy between findings is not immediately obvious. One possibility may be the use of neurologically normal volunteers in the present study (and in other imaging studies; see discussion in Bartolo et al., 2006).

The present findings thus suggest that the neural circuit for humor comprehension may include distinct components for the detection and resolution of incongruities. In this emerging account, the right MTG and right MFG may subserve the processes through which incongruities are detected, while activity in the left SFG and left IPL may handle the semantic integration required to resolve the incongruities. These results are consistent with Jung-Beeman's recent discussion of bilateral processes for comprehending natural language (Jung-Beeman, 2005). Finally, consistent with our earlier study (Chan et al., 2012) and with earlier research (Bartolo et al., 2006; Derks et al., 1997; Svebak, 1982), the present study found that humor processing involves both the left and the right hemisphere, and both the cortex and the subcortex.

In summary, the experimental design employed in the present study showed potential in identifying the neural substrates of the "incongruity detection" and "incongruity resolution" processes associated with the comprehension of verbal jokes. The association observed here between incongruity-related processing and activity in the right MTG and the right MFG further supports the claim that processing related to incongruity detection is located in this area. The present study also found that incongruity resolution is associated with activity in the left SFG and left IPL in the fronto-parietal regions. In addition to the funny and unfunny conditions, our earlier study (Chan et al., 2012) included a garden path condition as a baseline, whereas the present study included an additional nonsensical condition as a baseline. This difference may explain the finding of activation in bilateral IFG in our earlier study, but not in the current study. We plan to make a combined analysis of the two datasets to further investigate the similarities and differences between the two studies.

The present results, along with those from our earlier fMRI experiment using the comprehension–elaboration theoretical framework (Chan et al., 2012), suggest a distinct neural circuit subserving the comprehension (incongruity detection and resolution) and elaboration phases of humor processing. Fig. 6 displays the components of this circuit and the processing stages it supports. Within this neural circuit, the comprehension of verbal humor starts with the processing of semantic meaning and the identification of incongruities in the right MTG and right MFG, followed by semantic selection and integration associated with the resolution of these incongruities in the bilateral inferior frontal gyri, left SFG and left IPL. Finally, the left ventromedial prefrontal cortex and right anterior cingulate cortex and the subcortical bilateral amygdalae and bilateral parahippocampal gyri appear to be responsible for the affective response to humor during the elaboration stage (Chan et al., 2012).

Within the framework of the proposed three-stage neural circuit model of verbal humor processing, extended studies on this topic could be conducted by comparing sex differences in the neural correlates of incongruity detection and resolution during humor comprehension and in the inducement of the feeling of amusement during humor elaboration. Additionally, the data could be used as a baseline against which results from participants with Asperger's syndrome and schizophrenia syndrome could be compared to further investigate the neural substrates of humor comprehension and elaboration in different groups. Finally, studies could focus on verifying the neural circuit path

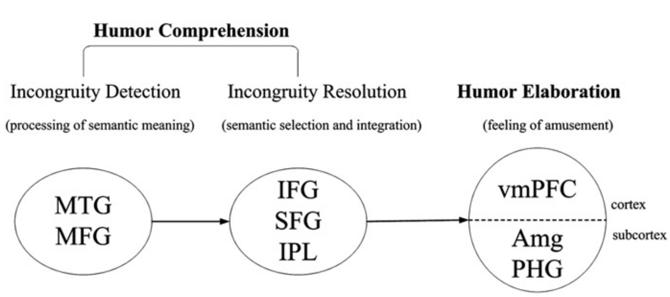

Fig. 6. Three stages of the neural circuit underlying comprehension and elaboration: incongruity detection and incongruity resolution during comprehension, and inducement of the feeling of amusement during elaboration. MTG = middle temporal gyrus; MFG = medial frontal gyrus; IFG = inferior frontal gyrus; SFG = superior frontal gyrus; IPL = inferior parietal lobule; vmPFC = ventromedial prefrontal gyrus; PHG = parahippocampal gyrus; Amg = amygdala.

model proposed above or on specifying additional components, in order to further develop our understanding of the neural circuit involved in the comprehension and elaboration process.

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