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Segregating the comprehension and elaboration processing of verbal jokes: An fMRI study

Yu-Chen Chan [a], Tai-Li Chou [b,c,d], Hsueh-Chih Chen [a,*], Keng-Chen Liang [b,c,d]

[a] Department of Educational Psychology and Counseling, National Taiwan Normal University, Taiwan
[b] Department of Psychology, National Taiwan University, Taiwan
[c] Neurobiology and Cognitive Science Center, National Taiwan University, Taiwan
[d] Graduate Institute of Brain and Mind Sciences, National Taiwan University, Taiwan

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ABSTRACT

The comprehension–elaboration theory of humor claims that the elicitation of humor can be segregated into two stages, comprehension and elaboration. Comprehension includes detection and resolution of incongruity, and elaboration involves inducement of the experience of amusement. Previous imaging research has sought to identify the neural substrates of humor processing by comparing funny and unfunny conditions. However, such studies have not been able to segregate the comprehension and elaboration stages. The present study was designed to differentiate the respective brain areas corresponding to comprehension and elaboration with an additional condition, garden path sentences. The results suggest that the bilateral inferior frontal gyri and left superior frontal gyrus may be associated with humor comprehension, whereas the cortical region in left ventromedial prefrontal cortex and the subcortical regions in bilateral amygdalae and bilateral parahippocampal gyri may be responsible for the feeling of amusement during the elaboration process.

1. Introduction

Humor is an important high-level cognitive activity that plays a crucial role in social life and also impacts various psychological and physiological phenomena (Goel and Dolan, 2001; Mobbs et al., 2003; Moran et al., 2004; Watson et al., 2007). Hence, exploring the neural substrates associated with humor may provide valuable information with a high potential for application.

To date most investigations of the neural processes associated with humor have been guided by the Suls' incongruity–resolution theory (Suls, 1972). Suls' theory can be illustrated through consideration of the traditional structure of a joke, which consists of a setup and a punch line. The setup is a short statement providing the details necessary to follow the joke and typically both explicit statements and implicit suggestions about the target of the joke. The setup is not intended to be funny, of course, because if it is funny, the punch line has nothing against which it can be contrasted. The punch line follows, generating humor through an unexpected 'twist' which is not congruent with the information in the setup (Attardo, 1997; Vaid et al., 2003; Wild et al., 2006). A new interpretation is then formed in order to resolve this incongruity between the punch line and the expectations established in the setup.

The present study, however, starts from the observation that not all situations involving the detection and resolution of incongruities are humorous. Corrected misunderstandings, scientific discoveries, silent responses to 'bad jokes', the interpretations of dreams and the resolution of garden path sentences all involve the juxtaposition of different frames and the subsequent re-establishment of coherence through acceptance of a new frame, *without humor being thereby generated*. This led earlier authors to develop an expanded theory of humor (Apter, 1982; Wyer and Collins, 1992). In Wyer and Collin's comprehension–elaboration theory of humor, comprehension refers to the detection and resolution of incongruities. As noted above, comprehension is necessary but not sufficient for humor. The elaboration follows comprehension, involves the conscious generation of inferences of features not made explicit during comprehension as well as further thoughts stimulated by the newly understood situation, and elicits the unconscious or conscious of feeling of amusement. These elaborations effectively involve appraising the stimulus event for their humorous content. The amount of humor elicited is a function of the amount of elaboration of the event and its implications that occur subsequent to its reinterpretation. The affective feeling of humor results from, and may overlap with continued elaboration of the event.

In the past decade, a number of studies have made use of functional magnetic resonance imaging (fMRI) technology along with other tools to isolate and identify the different neural regions involved in humor processing. To date, most of these fMRI-based studies of humor in normal subjects (Azim et al., 2005; Bartolo et al., 2006; Bekinschtein et al.,

* Corresponding author at: Section on Department of Educational Psychology and Counseling, National Taiwan Normal University, 162, Heping East Road, Sec. 1, Taipei, 10610, Taiwan. Fax: +886 2 23413685.
E-mail address: chcjyh@ntnu.edu.tw (H.-C. Chen).

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2011; Goel and Dolan, 2001; Mobbs et al., 2003; Watson et al., 2007; Wild et al., 2006), as well as studies of patients suffering from brain damage (Reiss et al., 2008; Schwartz et al., 2008; Shammi and Stuss, 1999) have adopted funny and unfunny conditions for comparison. These studies have identified a number of regions associated with surface-level semantic processing, incongruity detection and resolution and the affective response to humor. For example, Goel and Dolan (2001) had participants listen to semantic and phonological stimuli, comparing standard jokes with stimuli in which the punch lines were replaced with unfunny sentences. They found that the jokes activated brain regions in the left inferior frontal gyrus (IFG), bilateral posterior middle temporal gyrus (MTG), and left posterior inferior temporal gyrus (ITG). The subjects' post-scan funniness ratings of jokes revealed higher activation in the ventromedial prefrontal cortex (vmPFC) and bilateral cerebellum for jokes receiving higher ratings. Bartolo et al. (2006) also compared funny to unfunny cartoon stimuli and found that activation in the right IFG, left superior temporal gyrus (STG), left MTG, and left cerebellum was higher for funny cartoons. Comparing subjects' post-scan funniness ratings of jokes, they found activation in the left amygdala.

These studies represent important advances in our understanding of humor processing. At the same time, comparisons of funny and unfunny conditions inevitably conflate the comprehension (detection and resolution of incongruities) and elaboration (inferencing and humor appreciation) stages of processing. The present study makes use of a novel design which incorporates (non-humorous) garden path sentences. As garden path sentences require incongruity–resolution processing but do not elicit humor appreciation, the expectation was that they would make it possible to differentiate the neural substrates involved in the comprehension stage from those associated with the elaboration stage.

Garden path sentences refer to sentences that are grammatically correct, but which readers typically misinterpret in their first reading, leading to a semantic dead end (i.e., incongruity). Readers are then required to resolve this incongruity by re-reading the sentence to construct a sustainable interpretation (i.e., resolution of incongruity) (Christensen, 2010; Uchiyama et al., 2008). Garden path sentences thus require the same incongruity–resolution processing associated with humor comprehension, but not the processing required for appreciating humor associated with the elaboration stage.

It is generally agreed that, despite their diversity of surface meaning, all jokes are based on logical structure. Typically, a joke leads the readers along a garden path of expectation, but later the joke introduces an unexpected twist that entails a complete reinterpretation of all the preceding information. It is critical that the new interpretation makes as much 'sense' of the entire set of facts as the originally 'expected' interpretation. In this sense, garden path sentences have much in common with jokes (Ramachandran, 1998). In the present study, garden path sentences were incorporated in order to better understand humor processing. Non-humorous garden path sentences require incongruity–resolution processing, but do not elicit the feeling of amusement. The expectation was that the differences between garden path sentences and jokes would make it possible to segregate the neural substrates involved in the cognitive and affective components of humor. Our paradigm is similar to a humor study in Bekinschtein et al. (2011), in which jokes containing ambiguous words were compared with non-humorous sentences containing ambiguous words, as well as to matched verbal jokes not depending on semantic ambiguity (Bekinschtein et al., 2011). The condition of non-humorous ambiguous words is similar to our non-humorous garden path sentences. Many jokes are composed of disambiguated words with multiple meaning (Goel and Dolan, 2001). In the comprehension stage, the IFG and superior frontal gyrus (SFG) detect the unexpected incongruity and perform a semantic reanalysis in order to arrive at a meaning which would resolve the incongruity or utilize the so-called disambiguating mechanism to reach a satisfactory resolution (Jung-Beeman, 2005; Mason and Just, 2007). The IFG is involved in processing the semantic aspects of language comprehension and have been revealed in response to non-humorous semantically ambiguous sentences. Furthermore, greater activation in the left IFG is associated with processing ambiguities that are preceded by disambiguating context (Bekinschtein et al., 2011; Rodd et al., 2005, in press; Zempleni et al., 2007).

The elaboration stage follows immediately after joke comprehension, and generates inferences which associate (humorous) attributes to the characters in the joke, producing the experience of amusement or humor appreciation. The feelings of amusement elicited by humor appreciation is likely associated with greater activation in brain regions associated with 'rewards', including the ventromedial prefrontal cortex (Goel and Dolan, 2001) and a more widespread network of subcortical regions associated with 'rewards', including the amygdala, hippocampus, parahippocampus, thalamus, anterior cingulate cortex (ACC), midbrain, and ventral striatum (Azim et al., 2005; Bekinschtein et al., 2011; Berns, 2004; Mobbs et al., 2003, 2005; Wild et al., 2003; 2006).

In an earlier effort to isolate the mechanisms underlying getting the joke and enjoying the joke, Moran et al. (2004) attempted to dissociate humor detection from humor appreciation by having participants view episodes of *Seinfeld* or *The Simpsons*. Using the laugh tracks, humor appreciation moments were defined by bursts of audience laughter and humor detection moments were defined as the 2-s period before the onset of each laughter event. The remainder of each episode served as the baseline condition. They found that humor detection moments were associated with increased activity in the left inferior frontal and posterior temporal cortices, and humor appreciation moments with increased activity in bilateral regions of the insular cortex and amygdala.

However, as the authors noted, there is certainly individual variability associated with both the detection and appreciation of humor for films. Two features distinguish our experiment from Moran et al.'s. First, in terms of experimental design, we included an independent measure, the unfunny stories, which served as our baseline measure. This could remove the confounding variable related to individual variation. Secondly, in terms of test materials, we used verbal jokes instead of films, meaning that our material was more semantic in nature. The present study thus made use of a different design in an attempt to differentiate the respective brain areas corresponding to humor comprehension and elaboration in the processing of verbal jokes, by comparing three conditions: funny, unfunny, and garden path. According to the "comprehension and elaboration" theory (Wyer and Collins, 1992) and the finding of previous neuroimaging studies of humor, laughter, and reward, we hypothesized that (non-humorous) garden path sentences, in comparison with nonjokes, would elicit increased activation related to comprehension in several brain regions, including the bilateral IFG and the left SFG. We also predicted that funny jokes, in comparison with garden path sentences, would elicit increased activation related to elaboration concerning the feeling of mirth with the cortex of the reward system in the ventromedial prefrontal cortex (vmPFC). Furthermore, we hypothesized that greater activation within the subcortex of the reward system, including the bilateral amygdalae and bilateral parahippocampal gyri, would be associated with the feeling of amusement.

2. Material and methods

2.1. Participants

Twenty neurologically healthy volunteers [10 males and 10 females aged 20–29 years, 23.40 ± 2.74 years (mean $\pm$ SD)] participated in this study. They were all right-handed as determined by the Edinburgh Handedness Inventory (Oldfield, 1971) and native Mandarin speakers. The study was approved by the Research Ethics

Committee of National Taiwan University Hospital, and all of the subjects gave their informed consent to participate before commencing the experiment.

2.2. Stimuli

Sixty stories in Mandarin Chinese were selected, including twelve stories for each of three different conditions: the funny, unfunny, and garden path story conditions. Twenty-four filler stories were also included. Each joke structure contained two components: the setup and the punch line. The setups were 110–130 characters in length (mean = 122.27) and the punch lines were 15–30 characters in length (mean = 22.06). The lengths were matched across conditions for the setups and the punch lines.

The funny jokes were designed to elicit comprehension–elaboration processing. For example,

> Setup: One day after work, a mother buys some donuts from a store close to her office. When she gets home, she says to her eldest son, "Peter, Mom brought some sweets home. You can take one donut to share with your little brother. Don't eat it all yourself!" So Peter takes the donut, thanks his mom, goes to his little brother and says,Punch line: "Hey, we have a donut to share! I'll take the circle, and you can have the hole!"

The unfunny condition and the garden path condition were created by replacing the punch line in the funny joke condition. The unfunny condition was generated by replacing the punch line with a regular sentence not requiring incongruity–resolution processing, like "Hey, we have a donut to share! I'll eat half and you can have the other half!" The garden path condition was generated by replacing the punch line with a garden path sentence requiring incongruity–resolution processing without obviously requiring elaboration processing (and thus not eliciting an intense funny feeling). For example,

> 我不吃巧克力甜甜圈才合我胃口。

> "I don't eat chocolate donuts are more to my taste."

(This is a direct translation into English from Mandarin Chinese; the sentence is grammatically correct in Chinese.) This sentence could be divided in two stand-alone sentences: "I don't eat chocolate donuts" is a grammatically correct sentence, while "donuts are more to my taste" is another one. Therefore, "donuts" could be the object in the first half of the sentence or the subject in the latter half. However, according to the Long-Words-First rule of reading (Yang and Chen, 1995), readers will first read the message "I don't eat chocolate donuts", then reach the words "are more to" and notice that the additional verb "are" makes the complete sentence incomprehensible, forcing them to go back to re-analyze the sentence as "I don't eat chocolate. Donuts are more to my taste."

In the present fMRI study, there were 24 jokes, 24 unfunny sentences, and 12 garden path sentences. The unfunny condition and the garden path condition were created by replacing the punch line in the funny joke condition. To avoid lengthy scanning time, all participants only received 12 stories for each of three different conditions. The 60 jokes were chosen from a database of 120 jokes that had been established from a variety of sources like the internet, books and magazines, and the joke materials from previous literature. To ensure that the collected jokes were representatives of humor, the joke database was evaluated by 454 university students. The mean of comprehension level was 8.27, and the standard deviation was .32 using a 9-point Likert scale (ranging from 1 = "extremely incomprehensibility" to 9 = "fully comprehensibility"). This result indicates that these jokes are comprehensible to participants. The mean of funniness level was 5.24, and standard deviation was .41. In this fMRI post-scan rating, the mean of comprehensibility was 8.27 ± .61 and the mean of funniness was 6.63 ± 1.34 for the 12 jokes. The results of post-scan ratings of only 12 sentences per condition were similar to previous pilot experiments. Prior to the fMRI experiment, a behavioral experiment was conducted. The materials for the experiment were rated by a separate group of 37 native participants (13 males and 24 females aged 22.38 ± 3.46 years) who received the same standardized instructions. Participants reviewed the stimuli in counterbalanced and randomized order on a computer screen using E-Prime software, on which participants pressed a button to progress from one stimulus to the next after each was rated. Each stimulus was rated on its degree of comprehensibility and on the funniness of the punch line using a 9-point Likert scale (ranging from 1 = "extremely unacceptable/unfunny" to 9 = "fully acceptable/funny"). For the punch lines, the reaction times for the garden path condition were significantly longer than in the other conditions. Moreover, the funny joke condition had comparatively higher rating scores on funniness than did the other conditions.

2.3. 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 60 verbal stimuli. The duration of each stimulus was 37.1, 39.3, or 41.6 s in random order with a jittered interstimulus interval (ISI) for 5.1, 7.3, or 9.6 s, respectively (Fig. 1). Within a stimulus, the setup was shown once for 20 s, after which the punch line was delivered, lasting 9 s. Thereafter, participants were asked to provide a subjective funniness judgment by pressing one of two buttons on a keypad in the participants' hand. Pressing the button beneath the index finger indicated 'funny' and pressing the button beneath the middle finger indicated 'not funny'. The use of hand for the button-press responses was counterbalanced 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 9 min and 50 s. The total duration of the experiment for each participant was approximately 45 min and 56 s. Before entering the fMRI scanner, participants were reminded not to move their heads if they laughed.

After the scanning session, all participants were interviewed and asked to rate the comprehensibility and funniness of all stimuli on a 1 to 9 scale (1 = incomprehensibility/not funny at all, 9 = very comprehensibility/very funny) that had been presented during the scanning session.

2.4. Image acquisition

Images were acquired on a 3-Tesla scanner (Medspec, Bruker, Ettlingen, Germany) equipped with a bird-cage quadrature head

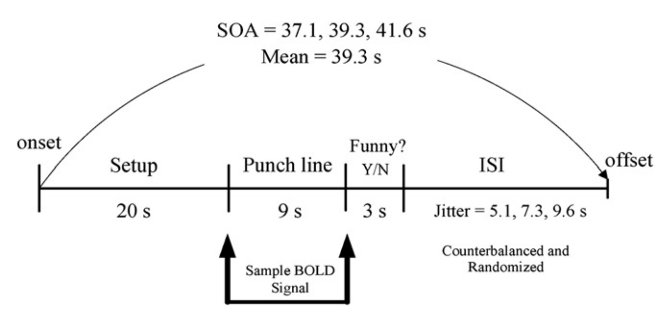

Fig. 1. Stimuli were presented in an event-related fMRI paradigm, with each verbal stimulus being presented in random. Stimulus-onset asynchrony (SOA) is the amount of time between the start of one stimulus and the start of another stimulus.

coil at 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 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 24 × 24 cm, and the matrix size was 64 × 64, giving an in-plane spatial resolution of 3.75 × 3.75 × 4 mm. Each functional run of acquiring 201 volumes took 9 min and 50 s. Data acquired during the first three TRs in each functional run were discarded to avoid T1 equilibrium effects.

2.5. 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. Coregistered 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 in the three experimental and filler conditions were treated as individual events for analysis and modeled for the punch line using a canonical hemodynamic response function (HRF). There were four event types: funny, unfunny, garden path, and filler. 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 garden path condition to the unfunny condition for humor comprehension, and the funny condition to the garden path condition for humor elaboration.

Given our a priori hypothesis based on previous imaging studies, a region of interest (ROI) analysis was performed (Poldrack et al., 2008). According to the finding of previous studies of humor, laughter, and reward, we used 13 hypothesis-driven ROIs with a radius of 10 mm centered at peak voxels of brain regions. The 13 ROIs included 10 regions based on Bekinschtein et al. (2011), 2 regions (bilateral parahippocampal gyri, PHG) based on Wild et al. (2006), and one region (left superior frontal gyrus, SFG) by Samson et al. (2009). The 5 ROIs related to humor comprehension included left dorsal inferior frontal gyrus (MNI coordinates: −45, 19, 25), right inferior frontal gyrus (36, 25, 3), left inferior temporal gyrus (−51, −49, −9), left anterior inferior frontal gyrus (pars triangularis; −52, 36, 6), and left superior frontal gyrus (−11, 11, 66). The 8 ROIs related to humor elaboration included ventromedial prefrontal cortex (MNI coordinates: 0, 45, −12), bilateral amygdalae (−23/23, −2/−2, −19/−19), bilateral ventral striatum (−16/16, 7/7, −7/−7), midbrain (0, −20, −11), and bilateral parahippocampal gyri (−18/18, −12/−12, −15/15). We then extracted the beta values from peak voxels of significant brain regions to partial out the contribution of the difference in behavior, including participants' reaction times as covariate.

To further evaluate the brain–behavior relationship, we also performed post-scan ratings on comprehensibility and funniness of the punch line for all participants. Participants were asked to rank each stimulus that they had found comprehensibility and funniness during the scan on a 1-to-9 Likert scale. Then, we split the stimuli into the high versus low comprehensibility conditions or the high versus low funniness conditions according to their rating scores. The contrast of the high versus low comprehensibility conditions was to examine comprehension-related increases in activation. The contrast of the high versus low funniness conditions was to examine elaboration-related increases in activation. All reported area of activation was significant at $p < 0.05$ FWE (familywise error) corrected for multiple comparisons at the voxel level, with a cluster size greater than or equal to 10 voxels.

3. Results

3.1. Behavioral results

In terms of funny/unfunny ratings during the scanning, the mean rating of "funny" responses was 85.59% for the funny condition, 15.59% for the unfunny condition, and 14.85% for the garden path condition. A one-way repeated-measures ANOVA on participants' rating scores was significant, $F(2, 38) = 131.81$, $p < 0.001$, and Bonferroni post-hoc tests revealed that the funny condition was significantly funnier than the unfunny and garden path conditions. There were no significant differences in the degree of funniness between the unfunny and garden path conditions. The reaction times (mean ± SD) for the funny, unfunny, and garden path conditions were 791.76 ± 165.09 ms, 1028.01 ± 295.34 ms, and 1240.89 ± 419.14 ms,

Table 1
Brain activations of 13 ROIs for the contrast of the garden path versus unfunny conditions and for the contrast of the funny versus garden path conditions.

Side	Region	Garden path versus Unfunny						Funny versus Garden path					
		BA	voxels	MNI coordinates			Z score	BA	voxels	MNI coordinates			Z score
				x	*y*	*z*				*x*	*y*	*z*	
L	Dorsal Inferior frontal gyrus	9	46	−42	11	25	4.71	–	–		–		–
R	Inferior frontal gyrus	47	21	33	27	1	3.80	–	–		–		–
L	Anterior Inferior frontal gyrus	46	28	−54	35	13	3.64	–	–		–		–
L	Inferior temporal gyrus	–	–		–			–	–		–		–
L	Superior frontal gyrus	6	21	−6	5	67	4.74	–	–		–		–
L	Ventral striatum	–	65	−15	8	−2	4.05	–	–		–		–
R	Ventral striatum	–	–		–		–	–	–		–		–
L	Ventromedial prefrontal gyrus	–	–		–		–	11	110	−6	47	−11	4.95
L	Amygdala	–	–		–		–	–	92	−33	−4	−23	4.83
R	Amygdala	–	–		–		–	–	87	24	−7	−26	4.69
	Mid-brain	–	–		–		–	–	–		–		–
L	Parahippocampal gyrus	–	–		–			28	61	−18	−19	−20	4.13
R	Parahippocampal gyrus	–	–		–			28/34	56	21	−10	−23	4.36

Note: MNI = Montreal Neurological Institute; L = left; R = right; BA = Brodmann's area; Voxels = number of voxels in cluster $p < 0.05$ FWE (familywise error rate) corrected at the voxel level, only clusters greater than or equal to 10 are presented.

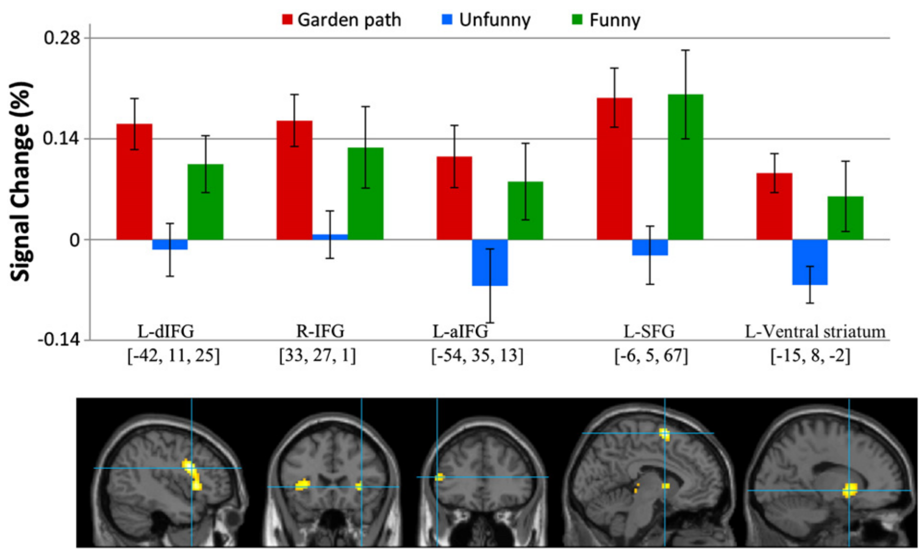

Fig. 2. Humor comprehension. Top: Bars show beta values for 5 regions of interest (ROIs) (peak voxels for each of the three conditions: garden path, unfunny, funny). Bottom: Sagittal or coronal brain images for the 5 ROIs. Greater activations were found for the garden path versus unfunny conditions in the 5 ROIs, including left dorsal inferior frontal gyrus (L-dIFG), right inferior frontal gyrus (R-IFG), left anterior IFG (L-aIFG), left superior frontal gyrus (L-SFG), and left ventral striatum (L-Ventral striatum).

respectively. A one-way repeated-measures ANOVA on reaction times was significant, $F(2, 38)=17.94$, $p<0.001$, and Bonferroni post-hoc tests revealed that reactions were significantly faster in the funny than in the unfunny condition, and that reaction times in the latter were significantly faster than for the garden path condition.

3.2. fMRI results

3.2.1. Stages in humor comprehension: the garden path versus unfunny conditions

With the use of ROIs, the contrast of the garden path versus unfunny conditions produced greater activation in the left dorsal inferior frontal gyrus (IFG, BA 9), right IFG (BA 47), left anterior IFG (BA 46), left superior frontal gyrus (SFG, BA 6), and left ventral stratum. After partiling for reaction times, the difference of the garden path versus unfunny conditions was significant in the left dorsal IFG ($F=58.80$, $p<.001$), right IFG ($F=42.77$, $p<.001$), left anterior IFG ($F=11.19$, $p=.006$), left SFG ($F=34.41$, $p<.001$), and left ventral striatum ($F=21.92$, $p<.001$). These results are summarized in Table 1 and Fig. 2.

3.2.2. Stages in humor elaboration: the funny versus garden path conditions

With the use of ROIs, the contrast of the funny versus garden path conditions produced greater activation in the left ventromedial prefrontal gyrus (vmPFC, BA 11), bilateral amygdalae, and bilateral parahippocampal gyri. After partiling for reaction times, the difference of the funny versus garden path conditions was significant in the left vmPFC ($F=29.17$, $p<.001$), bilateral amygdalae (left: $F=31.01$, $p<.001$; right: $F=13.29$, $p=.003$), and bilateral parahippocampal gyri (left: $F=11.73$, $p=.006$; right: $F=13.86$, $p=.002$). These results are summarized in Table 1 and Fig. 3.

3.2.3. Post-scan rating: the high versus low comprehensibility conditions

The contrast of the high versus low comprehensibility conditions produced greater activation in the left SFG (MNI coordinates: −9, 2, 73) and left anterior IFG (−45, 35, 10; Z=2.57, $p<.01$ uncorrected)

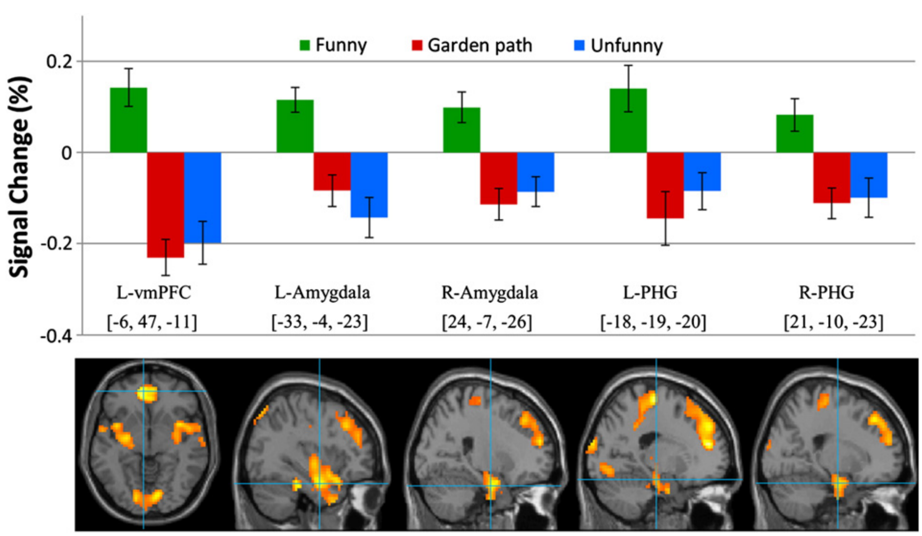

Fig. 3. Humor elaboration. Top: Bars show beta values for 5 regions of interest (ROIs) (peak voxels for each of the three conditions: funny, garden path, unfunny). Bottom: Horizontal or sagittal brain images for the 5 ROIs. Greater activations were found for the funny versus garden path conditions in the 5 ROIs, including left ventromedial prefrontal cortex (L-vmPFC), left amygdala (L-Amygdala), right amygdala (R-Amygdala), left parahippocampal gyrus (L-PHG), and right parahippocampal gyrus (R-PHG).

with the use of ROIs. The results were similar to those of the garden path condition versus unfunny path condition as shown in Table 1, providing further insight about the neural correlates of the comprehensibility of humor processes.

3.2.4. Post-scan rating: the high versus low funniness conditions

The contrast of the high versus low funniness conditions produced greater activation in the left vmPFC (MNI coordinates: −6, 53, −11), left amygdala (−24, −7, −23), right amygdala (24, −7, −29), left parahippocampal gyrus (−21, −13, −26), and right parahippocampal gyrus (21, −13, −23) with the use of ROIs. The results were similar to those of the funny condition versus garden path condition as shown in Table 1, providing further insight about the neural correlates of the amusement of humor processes.

4. Discussion

Most previous fMRI studies of humor used a funny condition and an unfunny condition as stimuli. However, comparisons of these two conditions have not been able to distinguish the neural substrates involved in the comprehension and elaboration stages of humor processing. Accordingly, the present study included garden path sentences as stimuli to elicit the incongruity–resolution processes associated with humor comprehension *without* activating the processes involved in elaboration or humor appreciation. Stories with funny punch lines were compared with matched unfunny stories with regular sentences replacing the punch lines and unfunny stories with garden path sentences replacing the punch lines. The results identified, for the first time, the distinct processes associated with comprehension and elaboration in humor processing.

Comparing responses to the garden path and unfunny conditions illuminates the humor comprehension stage. The obtained results confirm that the left IFG (Bekinschtein et al., 2011; Bornkessel and Schlesewsky, 2006; Mobbs et al., 2003; Moran et al., 2004; Rodd et al., 2005; Watson et al., 2007), right IFG (Bartolo et al., 2006; Bekinschtein et al., 2011; Rodd et al., 2005; Samson et al., 2009), anterior IFG (Bekinschtein et al., 2011; Goel and Dolan, 2001; Rodd et al., 2005) and left SFG (Bekinschtein et al., 2011; Samson et al., 2009) are involved in processing semantic aspects of incongruity–resolution. Our findings suggest that the IFG and SFG are responsible for incongruity detection, semantic decoding, semantic selection and semantic integration.

Verbal jokes are associated with verbal abstraction and mental schema shifting. The regions activated in the left hemisphere by language-dependent humor correspond strongly to the classical language areas, including Broca's area, anatomically described as the IFG (Friederici, 2002; Just et al., 1996). Recent fMRI studies have demonstrated that greater activation in left IFG is related to verbal jokes (Goel and Dolan, 2001), the humor and semantic ambiguity (Bekinschtein et al., 2011), the popular comic TV series *The Simpsons* (Moran et al., 2004), visual cartoons (Azim et al., 2005; Bartolo et al., 2006; Mobbs et al., 2003; Samson et al., 2009; Wild et al., 2006), and both verbal and nonverbal jokes (Watson et al., 2007).

Previous studies have shown that greater activation in left IFG may be associated with processing the semantic aspects of language comprehension and humor detection (Azim et al., 2005; Bekinschtein et al., 2011; Moran et al., 2004). Several studies also suggest that the left IFG is involved in resolving semantic ambiguities in semantically ambiguous sentences (Bekinschtein et al., 2011; Rodd et al., 2005, in press). Moran et al. (2004) used episodes of The Simpsons as humorous stimuli, and the onset of a laugh track as a marker between the humor comprehension and appreciation stages, and found that brain activity during the comprehension stage is characterized by left-lateralized activation in the left IFG and the left posterior temporal gyrus. The IFG of the left hemisphere is crucial for humor detection (i.e., getting the incongruity). In particular, the comprehension (i.e., resolving incongruity) is related to a more widespread network including regions of both hemispheres, including right IFG (Bartolo et al., 2006). Consistent with this finding, we found that bilateral inferior frontal gyri were active during incongruity–resolution processing in semantic aspects of language comprehension (e.g., resolving garden path sentences). The IFG appears to dominate in the incongruity–resolution process and generally in cognitive humor processing, especially the left IFG for language-related humor activation.

The cognitive processes underlying the resolution of verbal jokes seem to be a part of executive functions such as schema shifting, bridge inferences to reestablishment of context (Bekinschtein et al., 2011). The left SFG is involved in processing of incongruity–resolution humor, indicating that processing of humor comprehension requires more coherence building, as well as more mental manipulation and organization of context (Samson et al., 2009). Greater activation in the left SFG might be related to organizing thoughts, gaining insights, disambiguating and resolving the ambiguous sentences successfully. It might be possible that the left SFG is therefore involved in attempting to “making sense” or “attribution” (Samson et al., 2008).

Comparing the results of the funny condition to those of the garden path condition provides evidence concerning the elaboration stage. Previous studies of funny versus unfunny conditions have observed brain regions related to reward processing (Azim et al., 2005; Bekinschtein et al., 2011; Mobbs et al., 2003), such as vmPFC for affective appreciation of humor (Goel and Dolan, 2001). Moreover, many humor studies have demonstrated that various subcortical structures contribute to the feeling of amusement involving access to reward-related response in amygdala, nucleus accumbens, midbrain, ventral stratum, ventral tegmental area, and hypothalamus (Azim et al., 2005; Bekinschtein et al., 2011; Mobbs et al., 2003; Watson et al., 2007). Greater activations in amygdala (Azim et al., 2005; Bartolo et al., 2006; Bekinschtein et al., 2011; Kohn et al., 2011; Mobbs et al., 2003; Moran et al., 2004; Watson et al., 2007; Wild et al., 2006) and parahippocampal gyrus (Bartolo et al., 2006; Mobbs et al., 2003; Rodd et al., in press; Watson et al., 2007; Wild et al., 2006) have been associated with conscious self-reported amusement or the specific unconscious process of mirth. In the present study, greater activations in bilateral amygdalae and bilateral parahippocampal gyri were also positively correlated with the rating scores of funniness. Our findings further lend evidence to support the involvement of subcortical regions in humor elaboration process.

Interestingly, greater activation was found in the left ventral striatum related to humor comprehension process, not to humor elaboration process in the contrast of the garden path versus unfunny conditions. A possible interpretation is that the left ventral stratum may be activated due to the feelings of incongruity–resolution understanding that elicit relief of emotion reactions. This process may differ from the feelings of amusement. The garden path condition, which does not elicit humor appreciation, may require an extra “incongruity–resolution” component than the unfunny condition. In other words, the participants may feel surprised and unexpected for garden path sentences. They may try to resolve the incongruity to achieve coherence. The resolution of incongruity may result in the relief of emotion reactions. A future study could monitor autonomic reactions to disentangle relief from amusement of emotion reactions.

The present study also reveals that the activated areas related to humor processing are located in both hemispheres, and in both cortical and subcortical regions. This finding is consistent with earlier research (i.e., Bartolo et al., 2006; Bekinschtein et al., 2011; Mobbs et al., 2003). Svebak (1982) found coordinated activity across both hemispheres when participants watched a comedy film. Derks et al. (1997) also found activity in both hemispheres in an event-related potential study of joke comprehension and appreciation. In the present study, we found greater activation across the whole brain to deal with both comprehension and elaboration during humor processing.

The present findings suggest that the neural circuit for the stage of humor comprehension may be located mainly in the frontal lobe, with initial incongruity detection processed by the IFG and SFG in the left hemisphere, followed by semantic integration and resolution processed in the IFG in the right hemisphere. These results are consistent with Jung-Beeman's recent discussion of several lines of evidence pointing to the use of bilateral processes for comprehending natural language (Jung-Beeman, 2005). There it is suggested that, in addition to the well-established role of the left frontal and temporo-parietal regions, the right hemisphere may be involved in comprehending complex language. In particular, there is evidence that the right IFG may be involved in selection processes, especially when the information to be selected is activated more strongly in the right hemisphere (Knutson et al., 2004; Milham et al., 2001; Robertson et al., 2000). Similarly, Marinkovic et al. (2011) found a spatiotemporal progression from an initial attempt to process humorous puns in the left fronto-temporal area to a further stage of ambiguity detection and resolution in the medial prefrontal and right prefrontal areas.

In the following stage of humor elaboration, the left vmPFC in the cortical regions and bilateral amygdalae and bilateral parahippocampal gyri in the subcortical regions appear to subserve the process of humor appreciation that results in the feeling of amusement, as suggested in cortical regions by Goel and Dolan (2001), and in subcortical regions by Mobbs et al. (2003), Azim et al. (2005), and Bekinschtein et al. (2011).

5. Conclusions

The challenge of segregating the neural substrates of the comprehension and elaboration stages of humor processing, which cannot be met when only the funny and unfunny conditions are used in experimental designs, was attempted here via the novel experimental design of incorporating unfunny garden path sentences. It should go without saying that advanced studies are still needed to more fully segregate the comprehension and elaboration bases of humor. The present study has taken an initial step in this direction by distinguishing between two sets of neural substrates corresponding to two separate stages of humor processing, using three conditions: the funny, unfunny, and garden path conditions. The association observed here between humor comprehension and activity in the frontal regions of the bilateral IFG and the left SFG verifies that the main functions of incongruity detection, semantic selection, and semantic integration are located in this area. On the other hand, the vmPFC, bilateral amygdalae and bilateral parahippocampal gyri are related to the reward associated with the feeling of amusement. It remains to be discovered whether there are similar neural homologies in the mechanisms that underpin the other cognitive and affective processes which evoke humor. In addition, future studies could focus on investigating advanced humor comprehension process, distinguishing neural substrates of the incongruity and resolution cognitive process respectively in humor with finer definition, and verifying the neural circuit path mode for humor.

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