Humor Comprehension and Appreciation: An fMRI Study

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Abstract

■ Humor is a unique ability in human beings. Suls [A two-stage model for the appreciation of jokes and cartoons. In P. E. Goldstein & J. H. McGhee (Eds.), *The psychology of humour. Theoretical perspectives and empirical issues*. New York: Academic Press, 1972, pp. 81–100] proposed a two-stage model of humor: detection and resolution of incongruity. Incongruity is generated when a prediction is not confirmed in the final part of a story. To comprehend humor, it is necessary to revisit the story, transforming an incongruous situation into a funny, congruous one. Patient and neuroimaging studies carried out until now lead to different outcomes. In particular, patient studies found that right brain-lesion patients have difficulties in humor comprehension, whereas neuroimaging studies suggested a major involvement of the left hemisphere in both humor detection and comprehension. To prevent activation of the left hemisphere due to language processing, we devised a nonverbal task comprising cartoon pairs. Our findings demonstrate activation of both the left and the right hemispheres when comparing funny versus nonfunny cartoons. In particular, we found activation of the right inferior frontal gyrus (BA 47), the left superior temporal gyrus (BA 38), the left middle temporal gyrus (BA 21), and the left cerebellum. These areas were also activated in a nonverbal task exploring attribution of intention [Brunet, E., Sarfati, Y., Hardy-Bayle, M. C., & Decety, J. A PET investigation of the attribution of intentions with a nonverbal task. *Neuroimage, 11,* 157–166, 2000]. We hypothesize that the resolution of incongruity might occur through a process of intention attribution. We also asked subjects to rate the funniness of each cartoon pair. A parametric analysis showed that the left amygdala was activated in relation to subjective amusement. We hypothesize that the amygdala plays a key role in giving humor an emotional dimension. ■

INTRODUCTION

A Theory of Humor

> *Humor has been defined as ''. . .one element of the comic. . .[that] denotes a smiling attitude toward life and its imperfections: an understanding of the incongruities of existence'' (Ruch, 2001, p. 411).*

Recently, Suls (1972) proposed an ''Incongruity-Resolution theory,'' according to which the ability to comprehend humor is crucially dependent upon the ability to resolve the incongruity between the punch line and the expectations shaped by the storyline. This theory separates humor into two distinct states: surprise and coherence (Brownell, Michel, Powelson, & Gardner, 1983). Surprise is a feeling generated by an unexpected situation. To comprehend a joke, however, one must go beyond the state of surprise and formulate a new, coherent interpretation of the information.

The perceiver of the humor recognizes the incongruity between the punch line and what she was expecting and, consequently, embarks on a sort of problem-solving exercise, in which she/he is required to transform nonsense into humorous sense. Suls (1972) suggested that the resolution of this incongruity constitutes a problem-solving task. To transform an incongruous situation into a funny, congruous one, the subject must apply a logic, semantic, or episodic operator. The logic operator is employed in the processing of puns or riddles. The semantic operator is employed when comprehension of the humor depends on a semantic knowledge of the characters involved (e.g., political jokes). The episodic operator is generally applied in the processing of funny stories or comic cartoons, in which the subject has to revisit the episodes previously presented in order to understand the humor they are trying to convey.

To distinguish between the ability to get jokes and simple task-solving ability, Ruch and Hehl (1998) integrated Suls's two-stage cognitive model with another

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stage, that of detecting that the resolution is not really making sense as it is only an ''as-if'' resolution.

Patient and Neuroimaging Studies

A number of patient and neuroimaging studies of humor have been interpreted within the framework of the Incongruity-Resolution theory (Suls, 1972). However, results obtained in brain-damaged patients have not always been consistent with the findings produced by functional neuroimaging studies (for a complete review, see Wild, Rodden, Grodd, & Ruch, 2003).

Studies of patients found that those with right (RBD) rather than left brain damage (LBD) were more impaired in humor tasks, yet functional neuroimaging studies have stressed the role of the left hemisphere in processing humor. In particular, Bihrle, Brownell, Powelson, and Gardner (1986) found that the RBD patients performed worse than the LDB patients on both the verbal and nonverbal completion task. Furthermore, qualitative differences emerged between them with regard to the errors committed. In particular, in line with previous studies (Brownell et al., 1983; Wapner, Hamby, & Gardner, 1981), Bihrle et al. found that RBD patients retained a sensitivity to the surprise element of humor, but were less able to recognize coherence. Conversely, the LBD patients showed an impaired sensitivity to the surprise element of humor, but conserved the ability to integrate contents across parts of a narrative. Shammi and Stuss (1999) tested a series of brain-damaged patients and found that the patients most affected were the ones with right polar frontal lesions.

It is worth noting that patients with language deficits were often excluded from humor tasks. In particular, some authors excluded patients with left prefrontal lesions (Bihrle et al., 1986) on the grounds that the verbal task was too linguistically complex for them (Wapner et al., 1981). Also, a visual task was deemed too difficult for brain-lesion patients due to the number of visual details that had to be assimilated in order to detect the humor (Shammi & Stuss, 1999).

The first functional magnetic resonance imaging (fMRI) study of humor (in the form of verbal jokes) was carried out by Goel and Dolan (2001). These authors found that humor appreciation was associated with activation in the ventromedial prefrontal cortex (BA 10/11) and the bilateral cerebellum. They also separated phonological from semantic humor perception. Their results showed that phonological jokes (e.g., puns) activated the left temporal (BA 37) and left frontal gyrus (BA 44/45), whereas semantic jokes activated the right temporal (BA 21/37) and left temporal gyrus (BA 20/37).

Recently, Moran, Wig, Adams, Janata, and Kelley (2004) conducted an fMRI study using videos from the Seinfeld and Simpson series in order to dissociate humor detection (getting the incongruity) from humor appreciation (solving the incongruity). According to their findings, humor detection was associated with activation in the left inferior frontal and posterior middle temporal cortices, whereas brain activity during humor appreciation activated bilaterally the insular cortex and the amygdala. However, they did not ask subjects to rate videos as funny or not, and thereby failed to consider the wide variability of humor appreciation (Coulson & Kutas, 2001).

Mobbs, Greicius, Abdel-Azim, Menon, and Reiss (2003) presented a series of cartoons with captions and asked subjects to indicate whether they were funny or not. The authors found that humor detection engages a subcortical network, including, among others, the nucleus accumbens, which plays a key role in reward mechanisms (Schultz, 2002). They also found an activation cluster centered in the left temporo-occipital junction and extending into the fusiform gyrus (BA 37) (Mobbs et al., 2003). The authors claimed that this region was involved in processing the surprise element of jokes, playing a role in the early stages of the humor network. A second cluster, possibly related to processing linguistic coherence, was observed in a region including Broca's area (BA 44/45) and extending ventrally to the temporal pole (BA 38).

Overall, imaging studies demonstrate that humor comprehension is associated with activation of the left hemisphere, especially the temporal and frontal portions. However, this finding conflicts with the evidence derived from brain-damaged patients, who demonstrate a lack of humor comprehension following right rather than left hemisphere damage.

This conflict may be attributable to the material adopted to study humor comprehension. Indeed, the use of verbal material might constitute a bias for left hemisphere activation in neuroimaging studies (even though a left hemisphere lesion can affect story comprehension even in a nonverbal format) (Bihrle et al., 1986).

For these reasons, we believe that nonverbal material is more appropriate for studying the functional neuroanatomy of humor comprehension.

Nonverbal Cartoons and Theory of Mind

Previous studies including nonverbal cartoons were carried out to investigate brain-damaged patients' ability to attribute mental states (Happé, Brownell, & Winner, 1999), which is a Theory of Mind (ToM) skill (Premack & Woodruff, 1978). ToM includes, among others, the ability to infer beliefs, wishes, and intentions of other people in order to predict their behavior. In the study of Happé et al. (1999), the nonverbal material was characterized by single cartoons, where either false belief or ignorance to one or more of the characters in the picture was crucial for comprehension. Interestingly, attribution of mental state and attribution of intention activate different regions, as shown by the following two neuroimaging studies.

In an fMRI study, Gallagher et al. (2000) contrasted cartoons where the attribution of mental state (ignorance or false belief) was required to non-ToM cartoons. They found regions of increased brain activity in the medial prefrontal cortex bilaterally (BA 8), the right medial frontal gyrus (BA 6), the right temporo-parietal junction (BA 40), the precuneus (BA 7/31), and the fusiform gyrus (BA 20/36) bilaterally.

On the other hand, Brunet, Sarfati, Hardy-Bayle, and Decety (2000), using positron emission tomography, investigated the neural substrate involved in attributing intentions to others. They presented, in the upper half of the screen, a series of cartoon strips. Each series of three pictures described a short story. Three answer pictures were shown in the lower half of the screen. Subjects were asked to choose from these answer pictures the one showing the logical ending of the story. In one condition (attribution of intention to characters, AI), the correct picture could be guessed only by inferring the intentions of the characters, whereas in the other two conditions—involving physical causality with characters (PC-Ch) and with objects (PC-Ob), respectively—it was sufficient to comprehend the physical relationship of cause and effect. Comparison of the AI condition with PC-Ch showed increases of regional cerebral blood flow in the right medial frontal gyrus (BA 9), right inferior frontal gyrus (BA 47), right inferior temporal gyrus (BA 20), left superior temporal gyrus (BA 38), left cerebellum, bilateral anterior cingulate cortex (BA 24), and middle temporal gyri (BA 21).

For the study presented here, we devised an fMRI experiment involving the presentation to the subjects of either neutral or funny cartoon pairs. We did not make use of verbal humoristic material to circumvent the possible interference of linguistic processes.

In our funny cartoon pairs, the incongruity derives from a *disconfirmation* of the intentions initially attributed to the characters in the first cartoon. The expected ending is disconfirmed at the appearance of the second cartoon and, to reconcile with this incongruity, it is necessary to attribute to the cartoon characters a different intention. Processing of our funny cartoon pairs is therefore characterized by the following steps, illustrated in relation to Figure 1A and B:

Reading of the narrative schema, which generates an expectation: In Figure 1A, a person is drowning and another person is going to help him/her.

Detection of incongruity caused by a disconfirmation of the ending predicted on the base of the narrative schema: The first person is still drowning, but the other person is walking away (Figure 1B).

Resolution of the incongruity: The passerby did not intend to help the drowning person, but instead to steal his/her watch.

A feeling of amusement.

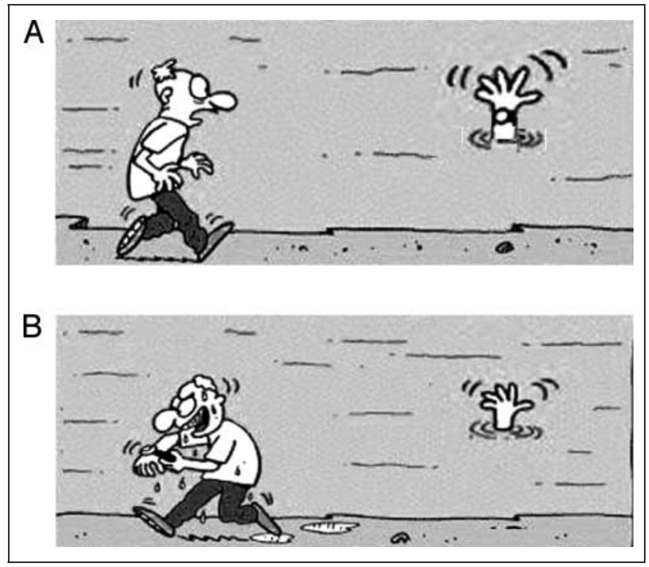

Figure 1. (A, B) Example of a funny cartoon pair.

We set out to investigate the different components of humor, that is, detection and resolution of incongruity and the feeling of amusement.

We anticipate that the achieved results suggest an involvement of both the right and left hemispheres in processing humoristic stimuli. Furthermore, we found activations of regions commonly involved in attribution of intention to characters (Brunet et al., 2000). We discuss this result in the light of a new approach to humor comprehension for episodic cartoons.

METHODS

Subjects

Twenty-one right-handed healthy volunteers, 8 men and 13 women, participated in this study. Their ages ranged from 23 to 36 years (mean age = 28.1 years, *SD* = 4 years; mean education = 14 years, *SD* = 2.3 years). Handedness was determined by means of the Edinburgh Inventory Scale (Oldfield, 1971). All the subjects had normal or corrected-to-normal visual acuity, and gave formal consent to participate in this study. The subjects were paid for their participation or received university credits. This study was approved by the Ethics Committee of the University of Modena and Reggio Emilia.

Material

The fMRI experiment was carried out using an event-related design. Each event stimulus consisted of two cartoons, a storyline begun in the first cartoon and ended in the second in either a funny or a neutral way (Figure 1A and B shows an example of a funny pair).

Seventy-two stimuli were initially chosen from an on-line database, containing different types of cartoon (www.tuttogratis.it/attualita/vignette_umoristiche_gratis.html). Then, to select the set of stimuli to be presented during the experimental sessions, 15 subjects were asked to rate the cartoon pairs on a scale of 0 (*not funny*) to 6 (*very funny*). Forty-three cartoon pairs rating >2.5 were included in the set of funny stimuli. Five independent raters checked the funny stimuli to include in the experimental set only those cartoon pairs requiring an effort to attribute intention to characters for the comprehension of the story. On this basis, 2 out of the 43 funny stimuli were excluded from the analyses.

Twenty-two cartoon pairs rating 0 formed the set of neutral stimuli. All the stimuli were in black and white. During the fMRI experiment, each subject performed five sessions, three including the presentation of nine funny and four neutral stimuli, and two the presentation of eight funny and five neutral stimuli. To get subjects acquainted with the task, they were administered a series of five cartoon pairs before the experimental phase. Visual stimuli were presented using a monitor positioned above the head coil (IFIS-MRI Devices, Wisconsin, USA). Responses were given using two buttons. Accuracy and response time data were collected during the scanning sessions by means of custom-made software developed in Visual Basic 6 (http://web.tiscali.it/MarcoSerafini/stimoli_video/).

Each event lasted for 18 sec, with stimulus beginning after 1.5 sec delay and cartoons remained on the screen for a duration of 3 sec each. A 0.5-sec interval elapsed between the presentation of the two cartoons making up each pair. Then a 10-sec interval followed. Overall each session lasted for 3.9 min.

To reduce movement artifacts, we have asked subjects not to laugh while they were inside the scanner. Subjects were instructed to indicate soon after the presentation of the second cartoon, by pressing one of the two response keys, whether the cartoon pairs were funny or not (Figure 2).

At the end of the acquisition session, out of the scanner, the subjects were asked to rate the same cartoons on a scale ranging from 0 (*not funny*) to 6 (*very funny*). They were asked to base their answers on how they had judged the cartoons while they were inside the scanner.

fMRI Data Acquisition

MRI data were obtained on a 3-T Philips Gyroscan Intera MR Scanner (Philips Medical Systems, Best, The Netherlands), using the standard setup of body coil transmission and SENSE head-coil reception.

Blood oxygen level dependent (BOLD)-sensitive fMRI images were acquired using a gradient echo-planar T2* sequence (TR = 1 sec, TE = 30 msec, FA = 80°, FOV = 220 mm, matrix 80 × 80, interpolated 128 × 128, SENSE factor = 2) from 16 axial slices of 2 mm thickness with an interslice gap of 1 mm. Therefore, a single event consisted of 18 volumes, for a total of 234 volumes in each session and 1170 for each subject. Dummy scans lasting 10 sec were acquired at the beginning of each session. Due to technical limitations, we decided to optimize the temporal resolution to the detriment of the amount of brain coverage. Therefore, we focalized our study on regions of most interest to us, namely, the mesial temporal and part of frontal lobes, renouncing to other regions possibly involved in the processing of humor (Moran et al., 2004; Mobbs et al., 2003; Goel & Dolan, 2001).

We also acquired high-resolution T1-weighted anatomical 3-D images from 170 slices of 1 mm thickness to allow anatomical localization (TR = 9000 msec; TE = 4 msec; FOV = 220 mm; matrix 256 × 256; voxel dimension 1.0 × 1.0 × 1.0).

Statistical Analyses

Image analyses were performed using SPM2 software (Wellcome Department of Imaging Neuroscience, London, UK). All functional volumes for each subject were realigned to the first volume, slice-time corrected, normalized to a standard echo-planar image template, and smoothed with a Gaussian kernel with full width at half maximum of 6 × 6 × 9 mm. For the event-related analysis, the appearance of the second cartoon was considered as the starting time of the stimulus of interest. Using statistical images achieved by single-subject analyses, we ran random effect group analyses (one-sample t test) contrasting the activation related with cartoons judged as funny with that of cartoons judged as not funny by the subjects in the scanner. Moreover, using responses collected out of the scanner, we ran a random effect second-level parametric analysis (one-

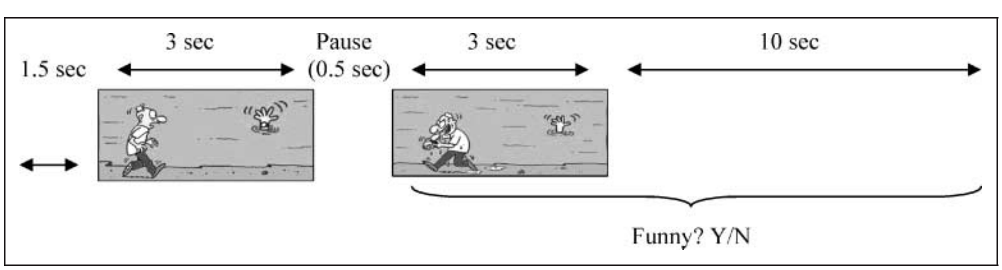

Figure 2. Single event-related design.

sample t test) to assess the activation associated to a subjective increase in the degree of amusement. A cluster of five or more voxels exceeding statistical threshold of $p < .001$ (not corrected) was considered significant foci of activation. The spatial coordinates in Talairach and Tournoux (1988) space were obtained applying the Matthew Brett correction (mni2tal: www.mrc-cbu.cam.ac.uk/Imaging/display_slices.html) to the SPM-MNI coordinates.

RESULTS

Behavioral Results (inside the Scanner)

The subjects were free to give their answers about considering a cartoon funny or not in their own time. Considering the five sessions as a whole, on average, subjects rated as funny 32.5 stimuli (SD = 6.2), and as not funny 31.9 (SD = 6.3). On average, their response times were faster for funny (2764 msec, SD = 698 msec) than for nonfunny stimuli (3065 msec, SD = 1016 msec).

fMRI Results

Stages in Humor Comprehension: Funny versus Nonfunny Stimuli

The appearance of the first cartoon generates an expectation that, in case of a neutral stimuli, is confirmed at the appearance of the second cartoon. On the contrary, with funny stimuli, the expectation is disconfirmed. Lack of confirmation generates an incongruity that has to be resolved reconstructing the story. In cartoon pairs, the incongruity relies on a process of attributing a different intention. The resolution of incongruity leads to a feeling of amusement.

Note that detection and resolution of incongruity (and the resulting feeling of amusement) intervene jointly during the presentation of the punch line. Consequently, in our paradigm, it was impossible to statistically separate these stages. Because we hypothesize that attributing intention intervenes in the resolution of incongruity phase, during presentation of the punch line, we expected to find, among others, the same areas that have been found activated in intention attribution tasks (Brunet et al., 2000). As the comparison of funny and not funny stimuli should include all of the three stages of humor, the remaining areas would be associated to the detection of incongruity, and feeling of amusement processes.

We run a random effect analysis contrasting the activation related with cartoons judged as funny with that of cartoons judged as not funny by the subjects. We found activations of both right and left brain regions, suggesting an involvement of both hemispheres in humor processing (see Table 1 and Figure 3A). Specifically, we found activation in the right inferior frontal gyrus (BA 47; peak Talairach coordinates, x, y, z: 51, 30, −17), the left superior temporal gyrus (BA 38; −32, 12, −28), the left middle temporal gyrus (BA 21; −55, 3, −20), and the left cerebellum (−34, −49, −18). These areas coincide with those found activated by attribution of intention tasks by Brunet et al. (2000), therefore confirming our hypothesis. Remaining areas should then be related to the other two phases of humor. In fact, like Goel and Dolan (2000), we found activation in the bilateral cerebellum, a structure identified as part of the network involved in laughter (Parvizi, Anderson, Martin, Damasio, & Damasio, 2001). Like Mobbs et al. (2003), we also found activation in the bilateral fusiform gyrus (BA 19/37), a region that, when electrically stimulated, has been found to induce laughter accompanied by a feeling of positive emotion (Arroyo et al., 1993). These areas could be related to the feeling of amusing that accompanied the resolution of incongruity. Furthermore, results showed activation of the left inferior frontal gyrus (BA 47; −51, 15, −8) and the left middle temporal gyrus (BA 21; −59, −11, −17) in response to the funny stimuli (Figure 3A). As suggested by the findings of Moran et al. (2004), the activation of these areas could be associated with humor detection.

Degree of Amusement: Parametric Analysis

To evaluate the network associated with subjective amusement, we ran a random effect second-level parametric analysis using subjects' ratings as independent variables. As shown in Figure 3B and Table 2, we found activations of the same regions we supposed to be involved in humor detection (left BA 47; −50, 23, −11; and left BA 21; −59, −10, −15). Also, we found activation in the right inferior frontal gyrus (BA 47; 51, 26, −14), the left middle temporal gyrus (BA 21; −55, 3, −20), the left superior temporal gyrus (BA 38; −30, 20, −26), and the left cerebellum (−32, −75, −16). This is the same circuit we hypothesized to be associated with attribution of intention from the results achieved in the previous comparison. Finally, we found activation of the left amygdala (−18, −5, −15), which has often been related to the processing of positive emotions (Lee et al., 2004; Hamann, Ely, Hoffman, & Kilts, 2002).

DISCUSSION

This study aimed at investigating the neural network involved in humor and in outlining the different stages in its comprehension and appreciation.

In the literature, imaging and patient studies have provided contrasting findings with regard to the side of the brain involved in humor tasks. Neuroimaging studies have emphasized the role of the left hemisphere (Moran et al., 2004; Mobbs et al., 2003; Goel & Dolan, 2001), and patient studies the role of the right hemisphere (Shammi & Stuss, 1999; Brownell et al., 1983; Wapner

Table 1. Brain Areas in which Stimuli-related BOLD Signal was Significant for Funny versus Nonfunny Cartoons

Regions and Brodmann's Areas	*No. of Voxels*	*Z Score*	*Coordinates* x	y	z
Left hemisphere					
Cerebellum, Fusiform Gyrus (BA 37)	190	4.61	−34	−49	−18
Superior Temporal Gyrus (BA 38)	56	4.59	−32	12	−28
Fusiform Gyrus, Inferior Occipital Gyrus (BA 19/18)	124	4.46	−32	−76	−14
Middle Temporal Gyrus (BA 21)	21	4.31	−59	−11	−17
Middle Temporal Gyrus (BA 21)	34	4.18	−55	3	−20
Superior Temporal Gyrus, Inferior Frontal Gyrus (BA 38/47)	85	3.97	−51	15	−8
Fusiform Gyrus (BA 20)	8	3.73	−40	−42	−23
Cerebellum, Fusiform Gyrus (BA 19)	9	3.63	−48	−69	−17
Fusiform Gyrus (BA 37)	9	3.56	−48	−42	−18
Right hemisphere					
Cerebellum, Fusiform Gyrus (BA 19)	418	4.49	6	−81	−24
Fusiform Gyrus (BA 36/37/20)	159	4.33	28	−45	−15
Superior Temporal Gyrus (BA 38)	24	3.94	34	22	−29
Inferior Frontal Gyrus (BA 47)	19	3.85	51	30	−17
Fusiform Gyrus (BA 19/37)	16	3.72	30	−59	−15
Cerebellum, Fusiform Gyrus (BA 19)	29	3.50	48	−67	−22
Fusiform Gyrus (BA 19)	23	3.49	51	−65	−14

p = .001, uncorrected.

$k > 5$ voxels.

et al., 1981; Gardner, Ling, Flamm, & Silverman, 1975). The advantage of neuroimaging studies is that they investigate the neural networks involved in humor processing in healthy people. However, studies performed to date have employed verbal jokes or nonverbal material with captions (Moran et al., 2004; Mobbs et al., 2003; Goel & Dolan, 2001). For this reason, they might be biased toward finding left hemisphere activation. Reports of several cases of humor comprehension impairment following right hemisphere lesions (Shammi & Stuss, 1999; Wapner et al., 1981) suggest that the role of this hemisphere may not have been adequately investigated by neuroimaging studies. Patient studies can allow inferences to be drawn about brain areas that are necessary for humor processing but have the great disadvantage of admitting only "certain" subjects to testing (i.e., those able to comprehend the task or to accomplish a thorough visual search). Thus, due to partial overlap and/or contiguity between humor and language networks, those studies might be biased toward emphasizing the role of the right hemisphere. The right hemisphere has been recognized as crucial for high-level language processing, such as metaphor comprehension (Bottini et al., 1994) or recognizing the moral of a story (Nichelli et al., 1995).

The use of nonverbal cartoons allowed us to circumvent any possible bias created by the use of verbal material. The results of this study showed involvement of both the right and the left hemispheres, and thus, overcame the discrepancy between patient and neuroimaging studies.

As reported previously, the theory proposed by Suls (1972) posits that humor comprehension involves two different processes: detection and resolution of incongruity. The resolution of incongruity is accompanied by a feeling of amusement. In our experiment, detection and resolution of incongruity stages co-occur during the presentation of the punch line, and these different stages are impossible to separate in the analysis. In our cartoon pairs, the intention predicted in the first cartoons was disconfirmed at the presentation of the second cartoon. The only way to understand the overall meaning of the cartoons' pairs was therefore to reconsider the character's previous intention. For this reason,

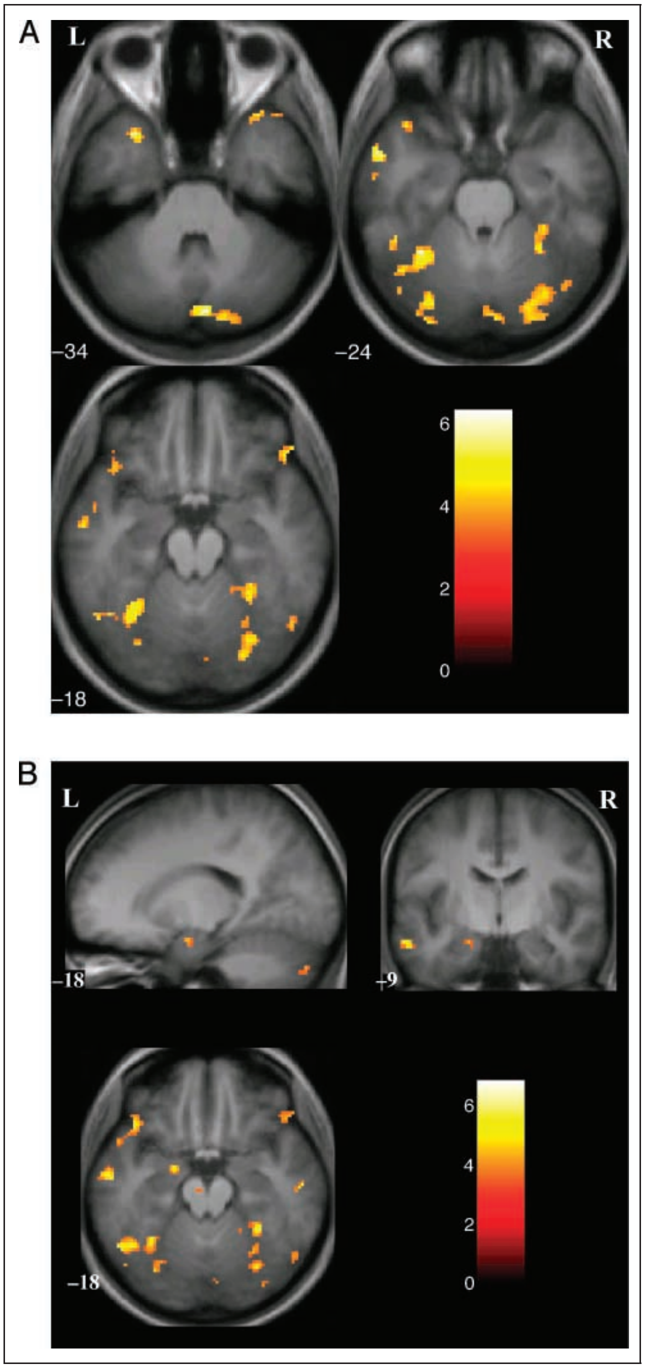

Figure 3. (A) Brain areas activated in response to funny versus nonfunny cartoons. Activated blobs are overlaid on a structural image obtained as the average of all the subjects' T1 volumes. (B) Brain areas activated during humor appreciation (parametric). Activated blobs are overlaid on a structural image obtained as the average of all the subjects' T1 volumes.

we hypothesized that some of the regions we should have found when comparing activation for funny and nonfunny cartoons should have been the same involved in incongruity resolution (attribution of intention). The remaining areas could have been related to incongruity detection and to feeling of amusement.

Comparing brain activations in response to funny versus nonfunny cartoons, we found activation of the right inferior frontal gyrus (BA 47), the left superior temporal gyrus (BA 38), the left middle temporal gyrus (BA 21), and the left cerebellum, a network of regions considered to be involved in attribution of intention. This finding suggests that attributing intentions could be an important step in the comprehension of humor of cartoon pairs. We hypothesize that it could be involved in the resolution of incongruity, as the types of cartoons would suggest. Indeed, in cartoon strips, the story could be fully understood when it is revisited under a process of attribution of intention. This result is also in line with studies in which right frontal brain-damaged patients had difficulty in establishing the coherence in a funny story, but not in detecting the incongruent element of the story (Bihrle et al., 1986; Brownell et al., 1983; Wapner et al., 1981). Indeed, right frontal patients can detect incongruity because the spared left hemisphere (frontal and temporal regions) subserves this ability, whereas they might fail to comprehend the meaning of jokes because their lesion encompasses part of the network used for solving the incongruity (Wapner et al., 1981).

We maintain that the remaining areas should be related to the others two phases of humor processing. In line with the findings of a neuroimaging study by Moran et al. (2004), we found activations in the left inferior frontal gyrus and in the left middle temporal gyrus. This result was also in line with the findings of a study by Bihrle et al. (1986). Using a series of funny and nonfunny captionless cartoon strips, these authors found that LBD patients are less sensitive to incongruity than RBD patients. Indeed, the patients with left hemisphere lesions were impaired in detecting the incongruity in a story. Together, our results, as well as these patient and neuroimaging findings, demonstrate the role of the left hemisphere, especially the frontal and temporal pole, in the detection of incongruity.

We were also interested in the feeling of amusing that accompanied humor, and accordingly analyzed brain activation in relation to the degree of amusement generated by items considered more or less amusing. We found activation of the same circuit involved in the attribution of intention (right inferior frontal gyrus, left superior temporal gyrus, left middle temporal gyrus, and left cerebellum). Suls (1972) argued that the central feature of humor is the resolution of incongruity, without which the humorous story, not understood, remains nothing more than an incongruous story: "There is humor when the parts of a joke make sense" (Suls, 1972, p. 83). Our results showed that, at least in our cartoon pairs, which require an episodic operator to resolve the incongruity, the degree of amusement generated is a function of the effort expended in attributing intentions to the cartoon's characters. As reported in Suls (1972), if a joke is very difficult to understand, it

Table 2. Brain Areas in which Stimuli-related BOLD Signal was Significant for Humor Appreciation (Parametric)

Region (Parametric)	No. of Voxels	Z Score	Coordinates *x*	*y*	*z*
Left hemisphere					
Cerebellum, Fusiform Gyrus (BA 19)	158	4.68	−32	−75	−16
Superior Temporal Gyrus, Inferior Frontal Gyrus (BA 38/47)	102	4.56	−50	23	−11
Fusiform Gyrus (BA 37)	194	4.53	−53	−57	−12
Superior Temporal Gyrus (BA 38)	73	4.24	−30	20	−26
Middle Temporal Gyrus (BA 21)	20	4.12	−59	−10	−15
Occipital Gyrus (BA 19)	15	4.08	−48	−69	−17
Amygdala	14	3.78	−18	−5	−15
Middle Temporal Gyrus (BA 21)	9	3.66	−55	−22	−9
Middle Temporal Gyrus (BA 21)	6	3.59	−55	3	−20
Cerebellum	13	3.45	−40	−42	−21
Middle Temporal Gyrus (BA 21)	5	3.44	−51	7	−23
Right hemisphere					
Cerebellum, Fusiform Gyrus (BA 18)	397	4.65	6	−81	−24
Fusiform Gyrus (BA 37/20)	86	4.44	30	−45	−13
Middle Temporal Gyrus (BA 21)	7	3.85	55	−18	−14
Fusiform Gyrus (BA 37)	23	3.79	28	−59	−15
Superior Temporal Gyrus (BA 38)	5	3.72	46	16	−36
Inferior Frontal Gyrus (BA 47)	16	3.51	51	26	−14
Parahippocampal Gyrus (BA 30)	8	3.48	16	−33	−6

p = .001, uncorrected.

$k > 5$ voxels.

would be considered not funny. The same happens to the cartoons for which the incongruity resolution is too easy, because it is too banal. The fact that parametric analysis demonstrated that areas of activation related to subjective amusement were the same involved in attributing intention—resolution of incongruity—is in line with the fact that the effort to resolve incongruity might have a role in rating funny a cartoon.

We also found that the degree of amusement is associated with activation of the left amygdala and the bilateral cerebellum. In humans, the amygdala (particularly the right-sided amygdala) is involved in negative emotions, such as fear (Benuzzi et al., 2004; Meletti et al., 2003; Nader, Schafe, & Le Doux, 2000). On the contrary, according to some studies, the left amygdala might be involved in positive emotions (Lee et al., 2004; Hamann et al., 2002).

In their ''Seinfeld and Simpson'' fMRI study, Moran et al. (2004) attributed humor appreciation to bilateral activation of the amygdala. Comparing funny and nonfunny cartoons, Mobbs et al. (2003) also described activation of a subcortical network, commonly related to reward mechanisms. This circuit included the left amygdala, the ventral striatum/nucleus accumbens, and the hypothalamus. Goel and Dolan (2000), using verbal jokes, found activation in the ventromedial prefrontal cortex (BA 10/11), which is also part of the same dopaminergic reward system. However, they did not report activation of the subcortical network. Recently, Azim, Mobbs, Jo, Menon, and Reiss (2005), comparing activation during funny and nonfunny stimuli in men and women, found that women more than men showed greater activation of mesolimbic regions, including the nucleus accumbens.

Finally, we found that the degree of amusement was also related to bilateral activation of the cerebellum. The role of the cerebellum in humor needs to be further explored. On the basis of a single case report of a patient with pathological laughter, Parvizi et al. (2001) hypothesized that the cerebellum plays a modulating and coordinating role in the production of laughter. The cerebellum receives inputs from the limbic cortex, including the amygdala. According to Parvizi et al., it might modulate emotional responses (e.g., laughter and crying) according to the specific contexts in which triggering stimuli appear.

In conclusion, in this study, we have explored humor using nonverbal cartoon pairs. Even allowing for the experimental context, these stimuli share features with many everyday situations commonly considered to be funny. Hence, the humor of many day-to-day situations might be related to the resolving of incongruity created by unfulfilled expectations. We have provided some evidence that this may depend on a specific ToM skill (i.e., the attributing of intention to others). In particular, the inferior frontal and middle temporal gyri of the left hemisphere are crucial for humor detection (i.e., getting the incongruity). Humor comprehension (i.e., resolving incongruity) is related to a more widespread network including regions of both hemispheres (right inferior frontal gyrus, left superior temporal gyrus, left middle temporal gyrus, and left cerebellum). Finally, the left amygdala and the cerebellum seem to be involved in modulating the affective component of humor.

Overall, this study has the merit of proposing a possible role of the attribution of intention in resolving incongruity. However, our findings are limited, in that we do not compare two types of episodic cartoons, funny ToM cartoons and funny non-ToM; therefore, we think that the present results may be further extended in future studies comparing these two types of cartoons. In particular, according to our findings, we expect that they would differ only with respect to the resolution of incongruity process. Indeed, they both are funny cartoons for which detection of incongruity and feeling of amusement would be present. However, in funny ToM cartoons, we would expect to find areas related to attribution of intention, whereas funny non-ToM cartoons would recruit different regions.

Another intriguing aspect of humor is denigration. In some cartoons and jokes, one or more characters act at the expense of one or more other characters in the story. It follows that to find a cartoon funny, the perceiver must not empathize with the subject or subjects who are on the receiving end of the actions. Further study should focus on the relationship between the feelings aroused by the characters who are placed at a disadvantage and the ensuing sense of amusement. This would give humor its social connotations.

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