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Cognitive humor processing: Different logical mechanisms in nonverbal cartoons—an fMRI study

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Abstract

Although recent fMRI studies on humor have begun to elucidate cognitive and affective neural correlates, they weren't able to distinguish between different logical mechanisms or steps of humor processing, i.e., the detection of an incongruity and its resolution. This fMRI study aimed to focus in more detail on cognitive humor processing. In order to investigate pure incongruity resolution without preprocessing steps, nonverbal cartoons differing in their logical mechanisms were contrasted with nonhumorous pictures containing an irresolvable incongruity. The logical mechanisms were: (1) visual puns (visual resemblance, PUNs); (2) semantic cartoons (pure semantic relationships, SEMs); and (3) Theory of Mind cartoons (which require additionally mentalizing abilities, TOMs). Thirty cartoons from each condition were presented to 17 healthy subjects while acquiring fMR images. The results reveal a left-sided network involved in pure incongruity resolution: e.g., temporo-parietal junction, inferior frontal gyrus and ventromedian prefrontal cortex. These areas are also involved in processing of SEMs, whereas PUNs show more [...]

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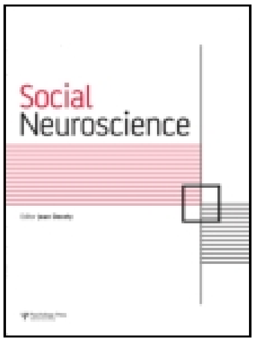

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Cognitive humor processing: Different logical mechanisms in nonverbal cartoons—an fMRI study

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Although recent fMRI studies on humor have begun to elucidate cognitive and affective neural correlates, they weren't able to distinguish between different logical mechanisms or steps of humor processing, i.e., the detection of an incongruity and its resolution. This fMRI study aimed to focus in more detail on cognitive humor processing. In order to investigate pure incongruity resolution without preprocessing steps, nonverbal cartoons differing in their logical mechanisms were contrasted with nonhumorous pictures containing an irresolvable incongruity. The logical mechanisms were: (1) visual puns (visual resemblance, PUNs); (2) semantic cartoons (pure semantic relationships, SEMs); and (3) Theory of Mind cartoons (which require additionally mentalizing abilities, TOMs). Thirty cartoons from each condition were presented to 17 healthy subjects while acquiring fMR images. The results reveal a left-sided network involved in pure incongruity resolution: e.g., temporo-parietal junction, inferior frontal gyrus and ventromedian prefrontal cortex. These areas are also involved in processing of SEMs, whereas PUNs show more activation in the extrastriate cortex and TOMs show more activation in so-called mentalizing areas. Processing of pictures containing an irresolvable incongruity evokes activation in the rostral cingulate zone, which might reflect error processing. We conclude that cognitive processing of different logical mechanisms depends on separate neural networks.

INTRODUCTION

Humor is an essential human characteristic and can be evoked by verbal (jokes) or visual materials (cartoons or movies), as well as in social situations. Cartoons are one common humor medium, showing pictures containing incongruous elements that have to be resolved in order to understand the punch line. In understanding cartoons, a stage of incongruity detection can be distinguished from a stage of incongruity resolution (e.g., Suls, 1972). First, the incongruity has to be detected in the cartoon, then it has to be resolved in order to understand the punch line of

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the cartoon. The incongruity resolution can be described as similar to a problem-solving process (e.g., Suls, 1972): A cognitive rule has to be found to bring two incongruous scripts together. Zigler, Levine, and Gould (1967) stated that the humor response depends on the demand that the stimulus makes on cognitive capacities. Cartoons can be classified in relation to formal or structural aspects (i.e., drawing style, resolvability of the incongruity, proportion of visual and verbal elements, etc.). There is evidence from several behavioral studies that formal as well as structural elements of the stimuli influence humor perception and processing (e.g., Herzog & Larwin, 1988; Huber & Leder, 1997; Ruch & Hehl, 1998; Samson & Huber, 2007).

Recent functional magnetic resonance imaging (fMRI) studies have sought to circumscribe areas that are involved in humor processing and its appreciation using jokes, cartoons or funny movies (e.g., Azim, Mobbs, Jo, Menon, & Reiss, 2005; Bartolo, Benuzzi, Nocetti, Baraldi, & Nichelli, 2006; Goel & Dolan, 2001; Mobbs, Greicius, Abdel-Azim, Menon, & Reiss, 2003; Mobbs, Hagan, Azim, Menon, & Reiss, 2005; Moran, Wig, Adams, Janata, & Kelley, 2004; Sieboerger, Ferstl, Volkmann, & von Cramon, 2004; Watson, Matthews, & Allman, 2006; Wild et al., 2006). A wide area around the temporo-parietal junction (temporo-occipital junction, posterior superior temporal sulcus, posterior middle temporal gyrus, in the following called TPJ), temporal pole and inferior frontal gyrus (IFG) is assumed to be involved in cognitive humor processing (e.g., Goel & Dolan, 2001; Mobbs et al., 2003; Moran et al., 2004; Wild et al., 2006). Most of the fMRI studies that have investigated neurologically healthy subjects found a more left-sided network. This might be due to the fact that the stimuli were most often purely verbal or verbal/visual. However, in their study, Wild et al. (2006) also found more left frontal activation with pure nonverbal stimuli.

The role of the TPJ in humor processing is interpreted controversially: Mobbs et al. (2003) claimed it to be involved in the detection of the incongruous element, whereas Azim et al. (2005) and Wild et al. (2006) assumed that the TPJ is involved in incongruity resolution. According to Moran et al. (2004), this area brings stored expectations online, whereas Watson et al. (2006) associated it with processing of social information in general.

The IFG (Goel & Dolan, 2001; Mobbs et al., 2003; Moran et al., 2004; Wild et al., 2006) and the temporal pole (Mobbs et al., 2003) have been claimed to be involved in the incongruity resolution process or generally in humor perception (Wild et al., 2006). Goel and Dolan (2001) circumscribed specific areas for different types of verbal jokes. Phonological puns activated areas that help to process sounds, i.e., the left inferior precentral gyrus and insula, whereas semantic jokes activated regions that process word meaning, i.e., the right posterior middle temporal gyrus (pMTG) and left posterior inferior temporal gyrus (pITG). Watson et al. (2006), using captioned cartoons, compared "sight gags", i.e., cartoons, in which the joke is based on elements in the picture (the cartoons remain funny, even if the caption is removed), to language-based humor (the cartoons are only funny when the caption is available). Visual-based humor activates among others bilaterally higher order visual cortex, TPJ, middle frontal gyrus (MFG) and precuneus. Language-based humor activates specifically the MTG, IFG and ITG.

Some studies segregated cognitive (i.e., comprehension of the humorous material) from affective (i.e., amusement, exhilaration induced by humorous stimuli and measured by funniness ratings) humor processing: The funnier the humor stimuli are perceived to be, the more activity can be found in the left insula, amygdala (Moran et al., 2004), pre-supplementary motor area (pre-SMA), dorsal anterior cingulate cortex (dACC; Mobbs et al., 2003) and in subcortical nuclei that belong to the dopaminergic reward system (Mobbs et al., 2003; Watson et al., 2006). Goel and Dolan (2001) and Sieboerger et al. (2004) found the ventromedian prefrontal cortex (vmPFC) and the cerebellum to be associated with funniness ratings. Several other frontal (i.e., left inferior frontal cortex) and parietal areas (i.e., left lateral parietal cortex) were also correlated with funniness ratings (e.g., Moran et al., 2004; Watson et al., 2006; Wild et al., 2006).

Two recent fMRI studies took individual differences in humor processing into account: Azim et al. (2005) investigated differences between males and females, Mobbs et al. (2005) showed that personality traits play a role in humor processing.

This brief summary of previous fMRI studies on humor processing reveals that there is a wide network involved in cognitive humor processing (e.g., the inferior frontal cortex, TPJ or

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anterior temporal areas). With the exception of the study by Goel and Dolan (2001), who sought to find separate modality-dependent pathways, or Watson et al. (2006), most fMRI studies compared humorous to nonhumorous stimuli without focusing in more detail on formal or cognitive elements of their stimuli. Further, no study attempted to investigate incongruity resolution without preprocessing steps as incongruity detection. Although Moran et al. (2004) distinguished a humor-detection process from a humor-appreciation stage, we have to emphasize, that their humor detection can not be equated to incongruity detection. Their humor detection includes incongruity detection as well as incongruity resolution and could be described as cognitive humor processing in general.

As a first goal of the present study, we attempted to circumscribe the network involved in pure incongruity resolution. Therefore, we separated different steps in humor processing: incongruity detection and its resolution. We presented not only a nonhumorous baseline that contained no incongruities or punch lines, but also an additional baseline condition. This additional condition consisted of pictures that did not contain a punch line, but led to the detection of an incongruity that couldn't be resolved. If you compare the irresolvable incongruity baseline with funny cartoons, you can contrast incongruity resolution (activity associated with funny cartoons) vs. preprocessing steps (such as the detection of incongruity, see Figure 1), as well as humor appreciation. It should be noted that affective aspects of humor processing were not the main focus of this paper.

A second aim of our study was to investigate cartoons differing in one formal element that determined the incongruity-resolution stage: According to the General Theory of Verbal Humor (GTVH; Attardo & Raskin, 1991), logical mechanisms (LM) describe the cognitive rule, how the incongruity of a joke or cartoon can be resolved. We presented three nonverbal stimuli conditions differing basically in their LM: visual puns (PUN), semantic cartoons (SEM) and Theory of Mind cartoons (TOM).

PUNs are analogous to verbal or phonological puns, as defined by Hempelmann (2004). PUNs are cartoons in which the punch line is based on the fact that one visual element activates two scripts that are incongruent to each other (Hempelmann & Samson, 2007). In the incongruity-resolution stage these two scripts have to be integrated, in terms of the GTVH (Attardo & Raskin, 1991), a script overlap has to be created (see Figure 1 for an example).

SEMs are cartoons that are based on pure semantic relationships in contrast to visual resemblance, as in PUNs. In SEMs, the incongruity lies in the opposition of two scripts based on pure semantic/content-related aspects. In order to resolve the incongruity, the perceiver has to recognize the LM that describes the relation of those scripts. In this stimuli group, several LMs are subsumed (e.g., exaggeration, juxtaposition, role exchange; Attardo, Hempelmann, & DiMaio, 2002).

TOM cartoons, as a third stimuli group, are a subgroup of SEM cartoons characterized by the fact that mentalizing abilities have to be involved in order to understand the joke. These cartoons are similar to false-belief tasks in the sense that the perceiver has to attribute mental states to the portrayed characters: The viewer has to recognize that one character does not know what the other character thinks or intends to do. The LM that circumscribes this requirement the best was defined by Attardo et al. (2002) and Paolillo (1998) as obvious error: ''A participant in the situation fails to recognize or acknowledge something exceedingly obvious or saliently presented'' (Attardo et al., 2002, p. 6; see Figure 1).

All three cartoon categories have in common that an incongruity has to be resolved, respectively, that two scripts have to be integrated, be it visually evoked or semantically. Whereas SEM can be seen as common cartoons, PUN and TOM can be described as stimuli that require more specific cognitive processes. According to Hempelmann (2004) the incongruity of phonological puns and semantic jokes is semantic, whereas the incongruity resolution of semantic jokes is purely semantic and the incongruity resolution of phonological puns is phonological and semantic. Translated into the visual world, the theoretical assumptions of Hempelmann (2004) would lead to the following predictions: Visual puns and semantic cartoons do not differ in their incongruity detection, but they do differ in their incongruity resolution. In contrast to SEM and TOM, for processing of PUNs it is not necessary to build a situation model (Zwaan & Radvansky, 1998) to get the joke, but it might be sufficient to detect and integrate two scripts that are revealed by one visual element. Therefore, PUNs are similar to pure picture play. To understand the joke, deep and complex processing of semantic

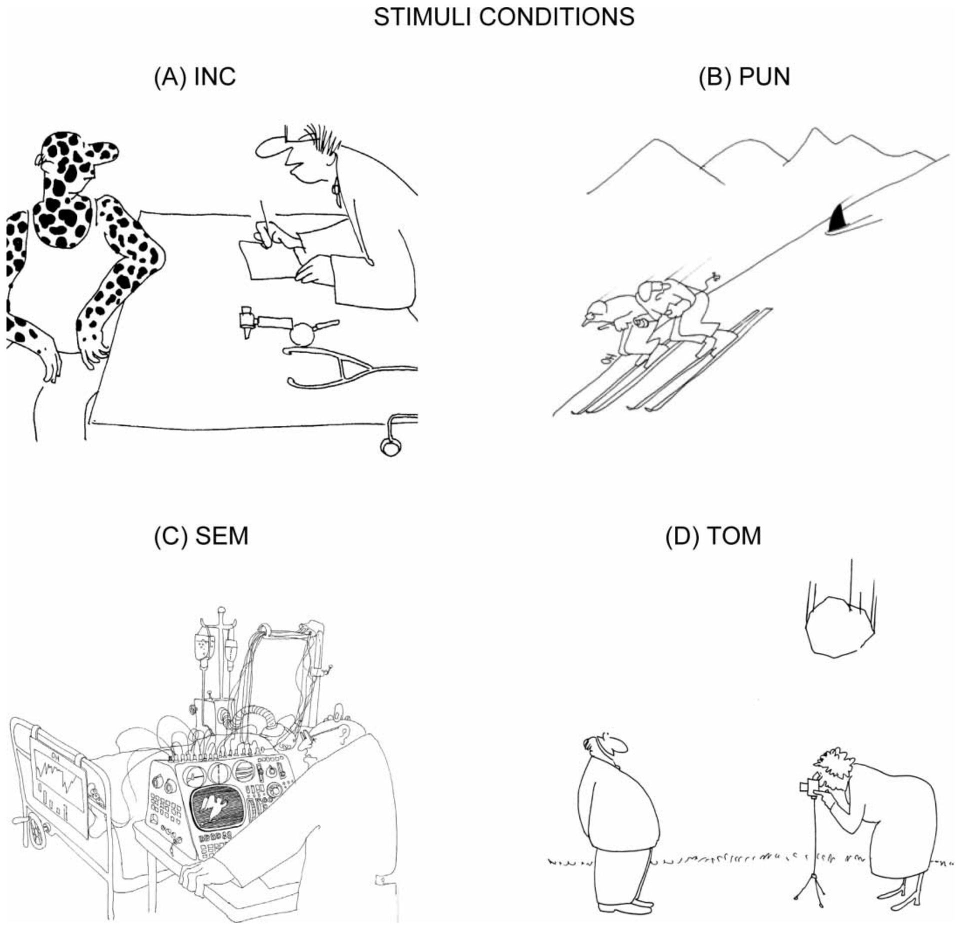

Figure 1. Examples of the stimuli used in the study. (A) A picture containing an irresolvable incongruity (INC). (B) A visual pun (PUN): one visual element (the diagonal line) can stand for the sea (activated through the fin) or the mountain (activated trough the skis). (C) A semantic cartoon (SEM): the joke is based on pure semantic relations and not on visual resemblance, as in PUNs: the patient has died which can be seen on the monitor in form of an angel flying away. There is no visual resemblance between the angel and the line which indicates no heartbeat. In order to understand the joke, no mentalizing abilities are required. (D) A Theory of Mind (TOM) cartoon: In order to get the joke, it is necessary to activate mentalizing abilities: to understand that the women does not know what will happen to her, while the man knows what will happen. Cartoons: Oswald Huber.

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relations is not necessary (see Hempelmann & Samson, 2007). Therefore, we expect to find more specific activations in PUNs, e.g., in higher order visual areas (extrastriate cortex). The comparison of the PUN and SEM conditions can be seen as a replication of the study by Goel and Dolan (2001) with pure visual, nonverbal material. As they found specific activation for processing of phonological puns, we expect to find in the PUN condition more activation in areas where visual features are processed.

In TOMs we expect to find more activation in typical mentalizing areas, as in the median PFC (mPFC), precuneus and particularly in the TPJ, analogous to Gallagher et al. (2000) or Marjoram et al. (2006). That TOM cartoons do require additional cognitive abilities to non-TOM cartoons is shown in their studies: Only processing of TOM cartoons required activation in the vmPFC, precuneus and TPJ bilaterally (Gallagher et al., 2000), or mPFC, precuneus, and temporal poles (Marjoram et al., 2006). These areas are typically associated with the attribution of mental states, whereas their non-TOM cartoons, described as ‘‘physical’’ (‘‘slapstick’’), didn’t require Theory of Mind or mentalizing capabilities for their correct interpretation. We have to underline, that their non-TOM cartoons are neither comparable to our SEM condition nor to our PUN condition. Slapstick humor is probably more based on incongruity than on incongruity resolution.

Two recent humor models postulated that mind reading is always part of humor processing (Howe, 2002; Jung, 2003). Howe (2002) stated

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that the essential element of humor is the observation and understanding of thought processes in the mind of the subject of a joke. If this hypothesis is true, typical mentalizing areas should be activated in the processing of any type of cartoons. A recent fMRI study on humor presented funny and unfunny cartoons to healthy subjects (Bartolo et al., 2006). As they found activation associated with the funny cartoons in some of the mentalizing areas (e.g., left superior temporal gyrus; STG), they hypothesized that incongruity resolution occurs with a process of intention attribution or mentalizing. However, they had no adequate control condition in order to prove that mentalizing is always involved in humor processing. In contrast to Howe (2002), Jung (2003) and Bartolo et al. (2006), we assumed that only in the TOM condition is it really necessary to activate mentalizing capabilities. Other humor types, for example visual puns or semantic humor, don't require taking the perspective of others and should therefore portray less activity in so-called mentalizing areas, particularly in medial prefrontal areas or in the TPJ.

To summarize, in this event-related fMRI-study we focused with pure nonverbal stimuli on regions that are specifically involved in incongruity resolution by means of contrasting "resolvable" cartoons with pictures containing an irresolvable incongruity. Further, we focused on the differentiation of LMs relating to incongruity resolution. In order to investigate this in more detail, we presented three groups of cartoons that differed in their LM: (1) visual puns, where the incongruity resolution process is visual/semantic; (2) semantic cartoons, where the incongruity resolution process is strictly semantic; and (3) TOM cartoons, where additionally Theory of Mind/mentalizing abilities are required to get the joke. The contrast PUN vs. SEM sheds light on different types of incongruity resolution (pure semantic or visual/semantic), whereas TOM vs. PUN/SEM might refute the hypotheses that claim that TOM is always involved in humor processing.

METHOD

Subjects

Seventeen right-handed and neurologically healthy subjects (9 female, 8 male; mean age 26.06 years; $SD = 3.25$) participated in this study. Written informed consent from all subjects was obtained prior to the scanning session. The study was conducted in accordance to the guidelines of the local ethics committee. All subjects had normal or corrected-to-normal vision and were native German speakers. None of the subjects were taking medication at the time of the study. Subjects were instructed prior to the actual experimental session. Once they felt comfortable with the task, subjects were positioned supine in the scanner.

Stimuli

In order to find and select appropriate stimuli, several pre-examinations were conducted. First, five subjects searched our own large cartoon collection and on the Internet for single-frame, nonverbal cartoons that intended to be primarily funny (not political) without sexual content, because the preference or dislike for sexual cartoons is known to correlate highly with certain personality characteristics (see, e.g., Ruch, 1998). Two hundred cartoons were selected and categorized independently by five raters into the groups of PUN, SEM, TOM and a rest category according to definitions that were given and explained to the raters. If at least four of five raters classified the cartoon into the same group (in 90% total agreement), they were used for further examinations. The 150 cartoons that were categorized into the groups of PUN, SEM or TOM were presented to 21 subjects (mean age $= 33.30$; $SD = 11.57$) to be rated for funniness, complexity and originality. From these cartoons, 90 were selected for the main investigation. The first criterion was a recognition time under 7 seconds. Second, the three conditions shouldn't differ regarding funniness ratings. However, PUNs were perceived to be less funny than SEMs and TOMs, which could be revealed by a repeated measure ANOVA: $F(2, 19) = 31.291$; $p < .001$. For the main investigation, PUNs with higher funniness values and SEMs and TOMs with lower funniness levels had to be selected. PUNs, as well as SEMs and TOMs below 7 seconds of recognition time were rank ordered along mean funniness scores. The 30 funniest PUNs were selected for the main investigation, as well as the 30 unfunniest SEMs and TOMs. Regarding complexity and originality, the three groups didn't differ significantly.

The stimuli for the two baseline conditions were drawn from a previous experiment (Samson, 2005): Pictures that were drawn in a cartoon or comic like manner without containing an incongruity or punch line (BAS) and pictures that contained an irresolvable incongruity (INC). These pictures were perceived to be not funny and to have high values in residual incongruity.

Task paradigms

The participants had to indicate per button press whether they understood the joke in the cartoon or not. This procedure was chosen in order to distinguish (a) cartoons that were understood but not funny from (b) cartoons that were not understood and therefore not funny. This allowed the exclusion of the non-understood cartoons or the understood INCs for further analysis. Comprehensibility responses were given via a button press with either the index (understood) or middle (not understood) finger of the right hand. The cartoons and pictures were presented for 6 seconds. The pictures were presented on a black screen (880×600 pixels), whereas the longer side of the picture had a maximum length of 500 pixels. For the stimulation of the visual cortex and the motor response, the baseline condition (BAS) was presented. In this condition, there were horizontal arrows in the right or left direction to indicate that the subjects needn't search for a punch line but had to press the right or left button. All conditions were presented in random order to prevent subjects from developing response tendencies.

All subjects processed 90 humor trials (30 PUNs, 30 SEMs, 30 TOMs) and additionally 30 INCs and 30 BAS. Further, 30 non-events were presented, giving a total of 180 trials for each subject. Trials were presented every 10 seconds on average, and a variable stimulus-onset delay (0, 400, 800, 1200 or 1600 ms) was introduced for trials in order to improve the temporal resolution (Miezin, Maccotta, Ollinger, Petersen, & Buckner, 2000); the stimulus-onset delay was balanced over the stimuli conditions. This gave a total time of 30 minutes for the experiment.

Stimuli were projected with an LCD-Projector onto a translucent screen behind the subject's head. The screen was viewed with mirror lenses attached to the head coil. If necessary, corrective lenses were mounted.

After the scanning procedure subjects were asked to rate the funniness of the 90 cartoons (PUN, SEM and TOM) on a computer-based experiment (Image_Rating) on a Likert scale from 0 to 6.

MRI scanning procedure

The experiment was carried out on a 3T scanner (Siemens TRIO, Erlangen, Germany).

For the cognitive paradigm, 26 axial slices ($3 \times 3 \times 3$ mm resolution, 0.75 mm spacing), parallel to the AC-PC plane and covering the whole brain were acquired using a single shot, gradient recalled EPI sequence (TR 2000 ms, TE 30 ms, 90° flip angle). One functional run with 900 time points was acquired, with each time point sampling over the 26 slices. Prior to the functional run, 26 anatomical T1-weighted MDEFT-images (Norris, 2000; Ugurbil et al., 1993) with the same spatial orientation as the functional data were acquired.

fMRI data analysis

The fMRI data were processed with LIPSIA software (Lohmann et al., 2001). This software package contains tools for preprocessing, registration, statistical evaluation and presentation of fMRI data.

Functional data were motion corrected offline with the Siemens motion correction protocol (Siemens, Erlangen, Germany). To correct for the temporal offset between the slices acquired in one scan, a cubic-spline-interpolation was applied. A temporal high-pass filter with a cutoff frequency of $1 = 120$ Hz was used for baseline correction of the signal and a spatial Gaussian filter with 5.65 mm FWHM was applied.

To align the functional dataslices onto a 3D stereotactic coordinate reference system, a rigid linear registration with six degrees of freedom (3 rotational, 3 translational) was performed. The rotational and translational parameters were acquired on the basis of the MDEFT slices to achieve an optimal match between these slices and the individual 3D reference data set. This 3D reference data set had been acquired for each subject during a previous scanning session. The 3D reference data set with 160 slices and 1 mm slice thickness was standardized to the Talairach stereotactic space (Talairach & Tournoux, 1988). The obtained rotational and translational parameters were normalized, i.e., transformed by linear scaling to a standard size. The resulting

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parameters were then used to transform the functional slices using trilinear interpolation, so that the resulting functional slices were aligned with the stereotactic coordinate system. Subsequently, a non-linear normalization was performed (Thirion, 1998). This step improved the spatial alignment of the individual neuroanatomy onto the neuroanatomy of a reference brain.

The statistical evaluation was based on a least-squares estimation using the general linear model for serially autocorrelated observations (see also Aguirre, Zarahn, & D'Esposito, 1997; Friston et al., 1995; Worsley & Friston, 1995; Zarahn, Aguirre, & D'Esposito, 1997). The design matrix was generated with a box-car function, convolved with a hemodynamic response function (HRF; gamma density function; Glover, 1999). The model equation, including the observation data, the design matrix and the error term, was convolved with a Gaussian kernel of dispersion of 4 s FWHM to account for the temporal autocorrelation (Worsley & Friston, 1995). In the following, beta-values were estimated for different contrast for each voxel. As the individual functional datasets were all aligned to the same stereotactic reference space, the resulting single-participant contrast-images were then entered into a second-level random effects analysis for the relevant contrasts. The group analysis consisted of a one-sample *t*-test across the contrast images of all subjects that indicated whether observed differences were significantly distinct from zero (Holmes & Friston, 1998). Subsequently, *t*-values were transformed into *Z*-scores. Images were thresholded at $z > 3.09$ ($p < .001$, uncorrected). Moreover, a region was considered significant only if it contained a cluster of 10 or more continuous voxels in the case of the contrasts of the LMs, respectively 19 or more continuous voxels in the main contrast—cartoons vs. INC (Braver & Bongiolatti, 2002; Forman et al., 1995).

RESULTS

Behavioral data

Table 1 reports the means and standard deviations from recognition time, comprehensibility response and funniness ratings.

Recognition time. A repeated measure analysis revealed significant differences between the four stimuli conditions INC, PUN, SEM and TOM; Mauchly's *W*.216, $\chi^2(5) = 22.537$, $p < .001$; Greenhouse Geisser, $F(1.562, 24.995) = 14.165$, $p < .001$. Bonferroni-corrected single comparisons yielded that INC differed from PUN ($p < .01$), but not from SEM ($p = .053$) and TOM ($p = .109$). PUN was processed significantly faster than SEM ($p < .05$) and than TOM ($p < .001$), whereas there was no difference between SEM and TOM ($p = .450$).

Comprehensibility response. A repeated measure analysis was conducted to investigate the comprehensibility response in dependence of the humor conditions (PUN, SEM and TOM) and the control conditions (BAS and INC) and yielded a significant main effect, $F(3, 48) = 159.755$, $p < .001$. Bonferroni-corrected single comparisons yielded no differences between the humor conditions PUN vs. SEM, SEM vs. TOM and PUN vs. TOM, but INC, as well as BAS differed significantly from all other conditions (for all comparisons $p < .001$), in the sense that they were less well understood.

Funniness. A repeated measure analysis was conducted to investigate funniness ratings in dependence of the three humor conditions, $F(2, 32) = 9.201$, $p < .01$. Bonferroni-corrected single comparisons yielded significant differences for PUN vs. SEM ($p < .05$), PUN vs. TOM ($p < .01$), but not for SEM vs. TOM ($p = 1.000$). As the cognitive processing of humorous cartoons stands in the main focus of our study, we won't report affective neuronal correlates in this article. However, in order to segregate affective from cognitive processing, post-scan ratings of funniness will be analyzed in order to replicate some

TABLE 1
Means and standard deviations for recognition time (in seconds), comprehensibility (0 = *not understood*, 1 = *understood*) and funniness ratings (from 0 = *not funny at all*, to 6 = *very funny*)

	Response		
	Recognition time	*Comprehensibility*	*Funniness*
Stimuli conditions	*M (SD)*	*M (SD)*	*M (SD)*
BAS	1.36 (0.52)	0.50 (0.02)	–
INC	4.62 (0.90)	0.24 (0.17)	–
PUN	3.81 (0.72)	0.84 (0.14)	2.37 (0.15)
SEM	4.10 (0.83)	0.85 (0.11)	2.88 (0.19)
TOM	4.22 (0.77)	0.85 (0.09)	2.95 (0.14)

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findings by, e.g., Goel and Dolan (2001) or Moran et al. (2004) and will be reported elsewhere.

To summarize, the behavioral data showed that INCs were processed significantly faster than all three stimuli conditions, as well as PUNs faster than SEM and TOM cartoons. INC and BAS differed significantly from all three stimuli conditions regarding comprehensibility as well as funniness, which was expected. Although the funniest PUNs were selected for the main investigation, they were perceived to be less funny than SEM and TOM cartoons. See the discussion section for possible reasons.

Imaging results

Incongruity resolution vs. irresolvable incongruity

In order to isolate brain structures that are only involved in successful humor processing (incongruity resolution), we contrasted the three humor conditions from the condition that contains an irresolvable incongruity. Figure 2 shows the resulting activation maps for cartoons vs. INC, and Table 2 reports the coordinates, volumes, maximum z-values and Brodman areas (BA) from the group-averaged data.

This comparison revealed significant activations for incongruity resolution on the left lateral side in the IFG, orbital part of the IFG and bilaterally (but more pronounced in the left side) in the TPJ (which involves the pMTG and posterior superior temporal sulcus, pSTS) and the supramarginal gyrus. That these areas are involved in incongruity resolution is strengthened through the circumstance that only cartoons that were understood entered the analysis. Likewise, the INC in which the subjects believed to have found a punch line were excluded for the analysis. Further, there was an activation in the vmPFC, which might be involved in the affective part of humor processing (cf. Goel & Dolan, 2001). In contrast, activations involved in the processing of pictures containing an irresolvable incongruity (INC) can be found in the left postcentral gyrus, precuneus, posterior cingulate cortex (pCC), collateral sulcus and left cerebellum. As well as in the rostral cingulate zone (RCZ) and on the right side, activations in the anterior MFG, extrastriate cortex and the anterior insula can be associated with processing of INCs. It is striking that the left frontal cortex is involved in successful humor processing, whereas the INC condition evoked activation only in the right frontal cortex.

SEM vs. PUN

In order to analyze which areas are involved in the different LMs, the PUN condition was contrasted with the SEM condition, which is defined to contain several semantic LMs that are not based on visual elements (as in PUNs). Figure 3 shows the resulting activation maps for PUN vs. SEM and Table 3 reports the coordinates, volumes, maximum z-values and BAs from the group-averaged data. The extrastriate cortex is more involved in PUNs than in SEMs, probably due to the fact that visual elements play a greater role in PUNs. Activations found only in the SEM condition were in the left precuneus, TPJ bilaterally, aSTS bilaterally, as well as the left cerebellum. This implies that the TPJ is much more involved in processing of SEM cartoons.

TOM vs. PUN

In order to highlight activations evoked through cartoons in which it is necessary to attribute mental states to portrayed characters in order to get the punch line, TOM was contrasted with PUN. Figure 3 shows the resulting activation maps for TOM vs. PUN and Table 4 reports the coordinates, volumes, maximum z-values and BAs from the group-averaged data. The following areas are involved particularly in TOM cartoons: right amPFC, right inferior frontal sulcus (SFS), left MFG and left superior frontal gyrus (SFG), precuneus, TPJ (extending to the extrastriate cortex and pMTG) bilaterally, right anterior lingual and fusiform gyrus as well as left aSTS. Processing of PUNs revealed activation in the left Ncl. caudatus. Interestingly, the right hemisphere is more strongly involved specifically for the TOM condition, compared to the activation maps in the contrast SEM vs. PUN.

TOM vs. SEM

The contrast TOM vs. SEM revealed no specific activation for SEM. TOM cartoons evoked activity in the bilateral precuneus, extending into the superior parietal lobe bilaterally

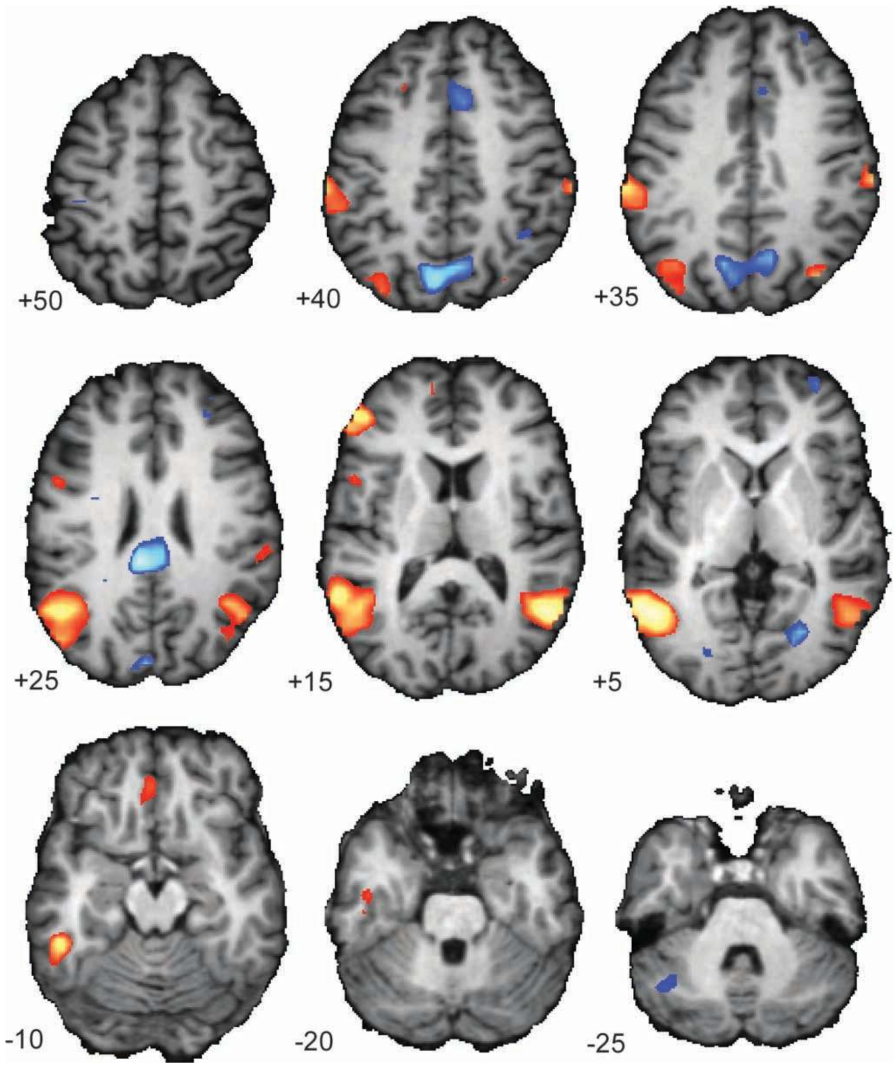

Figure 2. Contrast: Incongruity-resolution (funny cartoons) vs. irresolvable incongruity (INC). Significant regions of activation are projected onto the cortical surface of an average brain, obtained by nonlinear transformation of the participants' individual anatomies. Axial views are shown. All maps are thresholded at $z > 3.09$ ($p < .001$, uncorrected).

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and in the right TPJ, left TPJ (extending to the extrastriate cortex), activations in the right and left fusiform gyri and in the left cerebellum. There seems to be no qualitative difference between TOM and SEM, because there is no activation specifically for SEM. Figure 3 shows the resulting activation maps for TOM vs. SEM, and Table 5 reports the coordinates, volumes, maximum z-values and BAs from the group-averaged data.

To summarize, the contrast of funny cartoons vs. the baseline condition consisting of pictures containing an irresolvable incongruity, revealed activations in the IFG, TPJ and supramarginal gyrus bilaterally (but more pronounced in the left side), as well as in the vmPFC. Among others, activation in the RCZ can be associated with processing of irresolvable incongruity. Further, the results reveal differences in processing of cartoons with different LMs: PUNs evoke more activation in the extrastriate cortex, whereas SEM cartoons show more activation in the precuneus, TPJ, aSTS bilaterally and cerebellum. TOM cartoons reveal more activation in the amPFC, and other prefrontal areas, precuneus, TPJ and aSTS (in contrast to PUNs) as well as more activity in the precuneus, TPJ and fusiform gyri (in contrast to SEMs).

TABLE 2
Main activations CARTOONS vs. INC; Brodman areas, Talairach coordinates, volume and Z-maximum of the main activated regions

		Talairach coordinates			
Area	*BA*	*x*	*y*	*z*	*Volume (Z-max)*
Cartoons					
L ventromedian prefrontal cortex (vmPFC)	32	−8	29	−6	1134 (3.69)
L inferior frontal gyrus (IFG)	44	−50	5	18	1080 (4.79)
L inferior frontal gyrus pars orbitalis (IFGo)	10/46	−47	38	18	2268 (4.52)
L temporo–parietal junction (TPJ)	22/39	−59	−55	9	23220 (5.54)
R temporo–parietal junction (TPJ)	22/39	43	−58	18	10962 (5.46)
L supramarginal gyrus	40	−65	−31	36	3348 (4.48)
R supramarginal gyrus	40	61	−28	33	1377 (4.15)
INC					
R anterior middle frontal gyrus (aMFG)	10	31	56	6	1107 (−4.08)
R anterior middle frontal gyrus (aMFG)	9	25	38	27	2133 (−3.86)
R rostral cingulate zone (RCZ)	8/32	7	14	42	1647 (−4.00)
L postcentral gyrus	2/5	−47	−22	54	540 (−3.42)
L posterior cingulate cortex (pCC)	23	−5	−37	24	5616 (−5.43)
L precuneus	7	−8	−76	42	7587 (−4.65)
L collateral sulcus	19/18	−26	−76	9	2808 (−4.19)
R extrastriate cortex	19/18	25	−70	3	3537 (−4.75)
R anterior insula	–	28	17	9	918 (−3.47)
L cerebellum	–	−35	−61	−27	1782 (−3.86)

Notes: The volume is reported in mm^3 and z-values were thresholded at $z < 3.09$. Reported clusters contain at least 19 (513 mm^3) continuous voxels.

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DISCUSSION

This study revealed discrete characteristic patterns of cerebral blood-oxygen-level dependent (BOLD) activity induced by cartoons with different logical mechanisms in comparison to pictures that contain an irresolvable incongruity. Whereas the IFG could be confirmed to be involved in incongruity resolution (e.g., Goel & Dolan, 2001; Watson et al., 2006), we showed that the TPJ is involved in successful incongruity resolution and not in the detection of incongruity (e.g., Mobbs et al., 2003; Moran et al., 2004). Activity in the vmPFC reflects probably the affective response in humor processing, as in the studies by Goel and Dolan (2001) or Sieboerger et al. (2004). During the attempt to understand cartoons that don't contain a resolvable incongruity, there was activity in the RCZ, which is known to be activated during error processing (e.g., Ullsperger & von Cramon, 2001). The extrastriate cortex is activated particularly during processing of PUNs, whereas SEM cartoons evoked activity mainly in the TPJ, aSTS and precuneus. The TPJ bilaterally, amPFC as well as the precuneus—areas known to be involved in mentalizing—are more strongly activated during processing of TOM cartoons compared to PUNs, as well as to SEM cartoons.

Incongruity resolution vs. irresolvable incongruity

Our results revealed that incongruity detection and successful incongruity resolution are different processes requiring distinct areas. We were able to clarify the humor-associated role of the activity in the TPJ. In contrast to Mobbs et al. (2003) and Moran et al. (2004), we claim that the TPJ is not involved in early stages of humor processing, as in bringing stored expectations online or the detection of incongruity. We have shown the involvement of the TPJ in successful incongruity resolution, as Wild et al. (2006) already assumed. Although the attempt to resolve the incongruity is surely present in the INC condition, this effort does not, however, lead to successful humor processing and activation of the TPJ. This area appears to play a key role in the integration of complex featural information or multisensory integration (see Calvert, 2001, for a review) with connections to the limbic system (Barnes & Pandya, 1992). The TPJ also processes semantic

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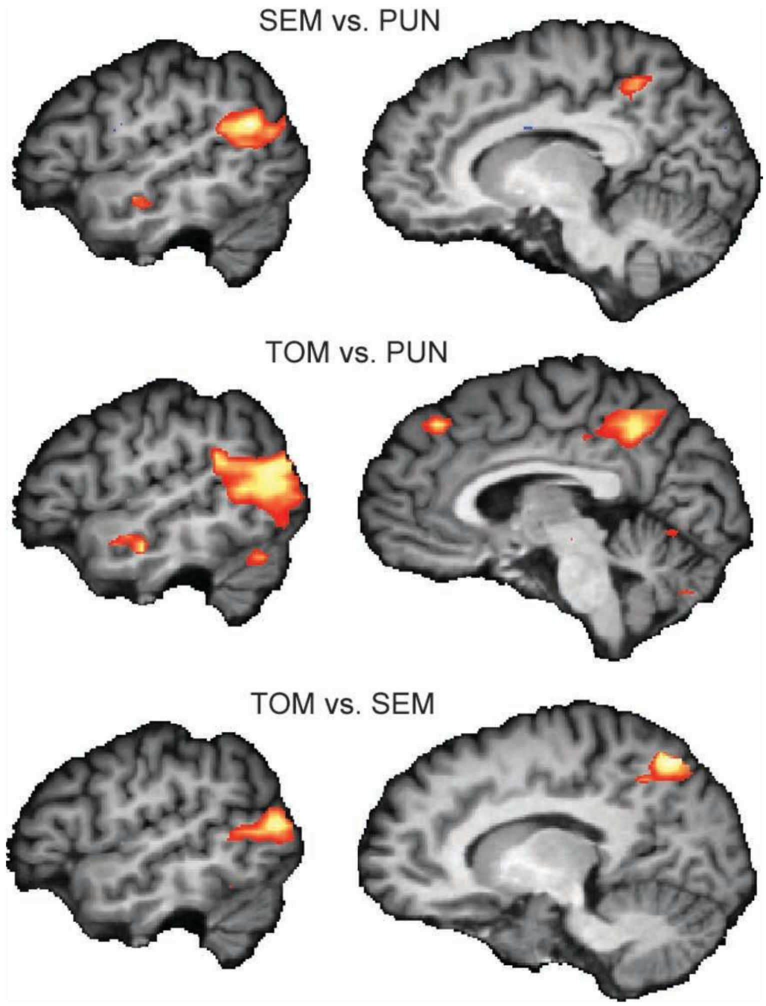

Figure 3. Significant regions of activation are projected onto the cortical surface of an average brain, obtained by nonlinear transformation of the participants' individual anatomies. In all three panels, sagittal views of the left lateral and medial cortices are shown. (A) SEM vs. PUN; (B) TOM vs. PUN; and (C) TOM vs. SEM. Slices for all lateral views through −50; slices in A medial −11, B medial +4, C medial +12. All maps are thresholded at $z > 3.09$ ($p < .001$, uncorrected).

integration of complex visual stimuli. Marjoram et al. (2006) suggested that the TPJ, although known to be one of the mentalizing areas, is involved in humor appreciation. Our contrast of the funny cartoons vs. INC shows that the TPJ is related to successful incongruity resolution. We suggest that this activation doesn't reflect amusement per se—which might be reflected rather in mesolimbic reward areas (see Mobbs et al., 2003) or vmPFC (e.g., Goel & Dolan, 2001)—but reflects the necessary cognitive component, i.e., successful incongruity resolution, of humor processing. Also, even with parametrical analysis of funniness ratings, other studies showed more activation in the TPJ the funnier a cartoon was perceived to be (e.g., Mobbs et al., 2003).

Increased activation in the left lateral PFC is also associated with humor processing (e.g., Goel & Dolan, 2001; Mobbs et al., 2003; Moran et al., 2004; Ozawa et al., 2000; Wild et al., 2006) and is interpreted as reflecting the incongruity resolution process. We were able to confirm that the IFG, known to be involved in language and semantic processing, is involved in incongruity resolution.

The data reveal that a left-sided network is involved in successful humor processing (i.e., the resolution of incongruity), which is in agreement with previous fMRI studies with healthy subjects. In particular, the left PFC seems to be essential, although some earlier lesion studies claimed that the right PFC might be involved in humor processing (e.g., Shammi & Stuss, 1999; see

TABLE 3
Main activations SEM vs. PUN; Brodman areas, Talairach coordinates, volume and *Z*-maximum of the main activated regions

Area	*BA*	*Talairach coordinates* *x*	*y*	*z*	*Volume (Z-max)*
SEM					
L precuneus	7	−11	−52	48	1755 (3.76)
L temporo-parietal junction (TPJ)	39	−50	−61	24	6372 (5.05)
R temporo-parietal junction (TPJ)	39	43	−49	24	6696 (5.03)
L anterior superior temporal sulcus (aSTS)	22	−56	−10	−12	918 (4.25)
R anterior superior temporal sulcus (aSTS)	22	46	−22	−6	459 (4.31)
L cerebellum	–	−26	−85	−24	1323 (4.76)
PUN					
R extrastriate cortex	19	−2	−88	36	405 (−4.09)

Notes: The volume is reported in mm^3 and *z*-values were thresholded at $z < 3.09$. Reported clusters contain at least 10 (270 mm^3) continuous voxels.

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Wild, Rhodden, Grodd, & Ruch, 2003, for a review). The more left-sided network is probably due to the fact that nonverbal pictures have to be verbalized during processing and that the same semiotic processes underlie humor processing independent of the presentation of verbal or visual material. Wild et al. (2006) also found more areas activated in the left hemisphere in processing of nonverbal cartoons. Particularly, it is striking that the left PFC is involved in incongruity resolution, whereas the right PFC seems to be involved in the processing of INC.

The RCZ is involved in unsuccessful humor processing or the processing of pictures containing an irresolvable incongruity: This activation might reflect conflict monitoring as described in several studies (see Botvinick, Cohen, & Carter, 2004, for a review) or increasing uncertainty (Volz, Schubotz, & von Cramon, 2003). Activation near our peak is associated with error detection or response competition (Ullsperger & von Cramon, 2001). Therefore, we assume that this activation reflects the conflict in which the several activated scripts are perceived as soon as the new information can't be integrated into the first script anymore, and the script opposition is detected. This might also explain why subjects need more time to process the INC condition: It might reflect cognitive effort required to decide definitively that there is no joke in the picture, or that they didn't understand the joke. Until they make this decision, they are uncertain whether

TABLE 4
Main activations TOM vs. PUN; Brodman areas, Talairach coordinates, volume and *Z*-maximum of the main activated regions

Area	*BA*	*Talairach coordinates* *x*	*y*	*z*	*Volume (Z-max)*
TOM					
R anterior medial prefrontal cortex (amPFC)	9	4	35	45	6966 (4.86)
R inferior frontal sulcus (IFS)	46	31	23	24	621 (4.22)
L middle frontal gyrus (MFG)	9	−35	29	39	270 (3.24)
L superior frontal gyrus (SFG)	8/9	−17	11	48	1134 (3.86)
R precuneus	31	7	−52	42	12744 (5.11)
L temporo-parietal junction (TPJ)	39	−38	−82	36	44307 (5.98)
R temporo-parietal junction (TPJ)	39	31	−76	33	30699 (6.44)
R fusiform gyrus	37	34	−58	−9	4509 (4.91)
R anterior lingual gyrus	19/37	16	−61	−3	1377 (3.56)
R temporal pole	38	37	14	−24	486 (3.51)
L anterior superior temporal sulcus (aSTS)	22	−50	−13	−15	1107 (4.75)
PUN					
L Ncl. caudatus	–	−11	14	15	270 (−4.02)

Notes: The volume is reported in mm^3 and *z*-values were thresholded at $z < 3.09$. Reported clusters contain at least 10 (270 mm^3) continuous voxels.

TABLE 5
Main activations TOM vs. SEM; Brodman areas, Talairach coordinates, volume and *Z*-maximum of the main activated regions

		Talairach coordinates			
Area	*BA*	*x*	*y*	*z*	*Volume (Z-max)*
TOM					
L precuneus, superior parietal lobe	7	−17	−67	48	1134 (3.87)
R precuneus, superior parietal lobe, TPJ	7	10	−70	51	12366 (5.23)
L temporo-parietal junction (TPJ)	39	−47	−76	15	11205 (4.92)
R fusiform gyrus	37	40	−58	−6	1728 (3.82)
L fusiform gyrus	37	−38	−46	−15	729 (3.76)
L cerebellum	–	−29	−82	−15	297 (3.65)
L cerebellum	–	−11	−79	−30	405 (3.85)

Notes: The volume is reported in mm^3 and z-values were thresholded at z <3.09. Reported clusters contain at least 10 (270 mm^3) continuous voxels.

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they missed the punch line. An additional explanation for this activation is also drive or motivation: Subjects have to continuously generate new hypotheses as to how the picture could be interpreted as a funny stimulus.

Differences in logical mechanisms

Our results reveal that there are crucial differences for the processing of different LMs or LM groups. Contrasting PUN from SEM, it is striking that there is more activation in the extrastriate cortex in PUNs. The visual element in PUNs evokes two scripts that stand ambiguously and simultaneously next to each other. Activation in the extrastriate cortex might be interpreted as the play with two meanings evoked by one visual element or associated with visual picture play. Further, this activation might be interpreted as reflecting visual adjustment processes for the processing of PUNs and that more visual cognition is involved in this LM. Also, Watson et al. (2006) found activation of higher order visual areas, associated with captioned cartoons in which the joke was based on elements portrayed in the picture and not contained in the caption. IFG activation in the study of Goel and Dolan (2001) was interpreted as being involved in the processing of sounds. Indeed, in our nonverbal paradigm there is no specific activation in the IFG for PUNs. Therefore, the IFG activation found by Goel and Dolan (2001) does not reflect specific activity for puns in general, but only for phonological puns.

Activations specific for SEM in contrast to PUNs are localized in the left precuneus, TPJ and aSTS bilaterally and left cerebellum. This corresponds mainly to the areas involved in incongruity resolution in general (cartoons contrasted with INC) and also replicates the results of Goel and Dolan (2001), who found more activation in the TPJ associated with semantic jokes.

Activity involved in PUN processing contrasted with TOM revealed a significant peak in the left nucleus caudatus.

It is striking that in the TOM condition—compared to PUN, but also to SEM—mainly the TPJ bilaterally, precuneus and fusiform gyri are involved. TPJ is known to play a specific role in attribution of mental states of others and not only when reading stories about people in physical detail (Saxe & Kanwisher, 2003). We claim that the TPJ is generally involved in the resolution of incongruity, but more so, when mentalizing is required in order to get the joke. Ferstl and von Cramon (2002) found activation in the TPJ not only during the TOM task, but also in the coherence condition, in which no Theory of Mind or mentalizing abilities were required in order to process the task. Therefore, it is plausible that the TPJ is involved also in the SEM condition. Perner and Aichhorn (2006) showed that the left TPJ is not specific for mentalizing tasks but also shows activity in perspective taking in nonmentalizing tasks. This might be similar to incongruity resolution or to switching between the two activated scripts of the joke.

The amPFC is essential for self-referential mental activity (Gusnard, Abudak, Shulman, & Raichle, 2001; Macrae, Moran, Heatherton, Banfield, & Kelley, 2004; Zysset, Huber, Ferstl, & von Cramon, 2002). The mPFC is engaged when we attend to our own mental states as well as those of others (Frith & Frith, 1999; see Frith & Frith, 2003, for a review). Since we found activation in the amPFC associated with TOM (in contrast to SEM), we assume that self-referential processes are more relevant in TOM cartoons.

Mentalizing and humor processing

As often in Theory of Mind tasks, we showed activation in the TPJ, precuneus and amPFC. As they are not present in the PUN condition, we claim that mentalizing is not always necessary to process humor. This contradicts two humor models that postulated the requirement of mind reading in all humor processing (Howe, 2002; Jung, 2003). We argue against these assumptions, otherwise we should also have found typical mind-reading areas such as the TPJ, precuneus or amPFC in the PUN condition activated to the same amount as in TOMs. This leads to the assumption that in PUNs the essential humorous element is to recognize that one visual element is compatible with two different meanings. Therefore, the activation in PUNs (vs. SEM) could be interpreted to be caused through visual picture play and more visual cognition, similar to logical problem-solving tasks based on physical/visual causality, whereas for SEM and TOM it is necessary to build a situation model. Therefore, capabilities to attribute mental states are required, particularly in the TOM condition. Further, Marjoram and colleagues (2006) suggested that mentalizing abilities and humor appreciation are both aspects of social cognition and therefore might show overlapping activations.

From our results, it can be concluded that different LMs are processed differently—PUNs in particular differ from SEMs and TOMs. Whereas there is a qualitative difference between PUN and SEM (a different processing network), there seems to be a gradational relation between SEM and TOM (the same network). Therefore, we conclude that different LMs require different cognitive processes additionally to a general incongruity resolution process, and it is fruitful to distinguish between different LMs in humor processing, as the GTVH postulates (Attardo & Raskin, 1991).

Interestingly, SEM and TOM don't differ regarding several rating scales for funniness, originality, complexity, etc. (Samson, 2005), while this study revealed differences in brain-activation patterns. This shows that it is fruitful to consider neuronal data in order to understand the nature of humor processing.

We suppose that the core element of humor is the resolution of an incongruity as described in several incongruity resolution or cognitive-linguistic theories (e.g., Attardo & Raskin, 1991; Suls, 1972), similar to a problem-solving process, whereas mind reading is an important factor that enhances funniness. In PUNs it is not necessary to construct a situation model, activate self-referential processes (e.g., Zysset et al., 2002) or mind-reading in order to get the joke. This might explain why PUNs are perceived to be less funny than SEM and TOM. We argue that there is less emotional involvement. PUNs can be quite "technical" and their LMs are somehow abstract. PUNs are perceived to be less sophisticated or less profound, or perceived as symbolic play.

In further studies it might be interesting to investigate in more detail the group of semantic cartoons that contain several LMs. Is it possible that the LM exaggeration is processed differently from LMs like juxtaposition, potency mappings, etc. (see Attardo et al., 2002)? Further, it would be interesting to compare nonverbal cartoons (particularly PUNs) to non-funny visual riddles or puzzle pictures, to clarify commonalities and differences of problem-solving and humor processing.

Furthermore, in order to better comprehend humor processing, it would be interesting to investigate whether the preference for certain LMs depends on personality traits similar to the fact that incongruity resolution and nonsense jokes depend on personality traits as, for example, conservativism (see, e.g., Ruch, 1998) or whether they score differently on other rating scales than funniness as other perceptual qualities of humor.

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