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Neural substrates of incongruity-resolution and nonsense humor

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ABSTRACT

By means of functional magnetic resonance imaging the present paper analyzes the neural correlates of processing and appreciating incongruity-resolution and nonsense cartoons. Furthermore, the relation between experience seeking and these neural substrates was investigated as this personality characteristic is known to influence humor appreciation. In the processing of incongruity-resolution stimuli the incongruity of the joke is largely resolvable, whereas in nonsense stimuli it is only partially resolvable and more incongruity remains. The anterior medial prefrontal cortex, bilateral superior frontal gyri and temporo-parietal junctions (TPJ) show more activation during processing of incongruity-resolution than of nonsense cartoons. These differences indicate that processing of incongruity-resolution cartoons requires more integration of multi-sensory information and coherence building, as well as more mental manipulation and organization of information. In addition, less self-reference might be established in nonsense cartoons as it is more absurd and more often deals with impossible situations. Higher experience-seeking scores correlate with increased activation in prefrontal, posterior temporal regions and the hippocampus. This might be due to a more intense exploration of the humorous stimuli as experience seekers tend to search novel mental stimulation. Furthermore, experience seeking was positively associated with brain reactivity towards processing nonsense in contrast to incongruity-resolution stimuli, which is in line with behavioral studies that showed a preference for nonsense humor by experience seekers.

1. Introduction

Laughter-related phenomena, such as humor, emerged probably through non-serious incongruity which is assumed to have been an indicator of social play and safety in early bipedal life (see Davila Ross, 2007; Gervais & Wilson, 2005). The relaxed open-mouth or "play" face is revealed in numerous other primate species (Preuschoft & van Hooff, 1997) which, if one accepts recapitulationist reasoning, leads to the idea that it served as a rudimentary precursor to human laughter. Humor as a universal human phenomenon encompasses numerous functions, such as an effective coping mechanism in the struggle with difficult situations throughout life but also as a useful communication tool in social situations. The latter is particularly successful if the communicating subjects are able to laugh about the same style of humor, as well as humorous contents. Laughter is one of the observable behaviors that accompany the humor process which consists of the cognitive processing of a stimulus and, usually, appreciation. Experiencing humor is understood here as a more cognitively sophisticated ability, involving the processing of incongruity with meaningful resolution. The present study investigates humor processing in relation to the resolvability of incongruity as a stimulus characteristic and in relation to experience seeking, as this personality characteristic is known to influence humor processing.

While intuitive and theoretical taxonomies typically distinguish content classes of humor, Ruch and colleagues (e.g., Ruch, 1992; Ruch & Hehl, 2007) used factorial analysis to show that structural aspects of humorous stimuli are at least as important as their content. In their studies, two factors that differ regarding structural characteristics consistently emerged: humor appreciation of incongruity-resolution and of nonsense jokes and cartoons (see below). Jokes and cartoons within each of these two groups may have different content (themes, targets) but are similar with respect to their structural properties and—presumably—in the way they are processed. Incongruity-resolution and nonsense stimuli (e.g., jokes and cartoons) put different loads on of different cognitive capacities which even influence the preference of one over the other depending on personality characteristics (see Ruch & Hehl, 2007). Thus, it is likely that the differentiation between stimuli that require incongruity-resolution and nonsense processing—which differ mainly regarding the resolvability of the incongruity—has an influence on the neural substrate of humor processing. The influ-

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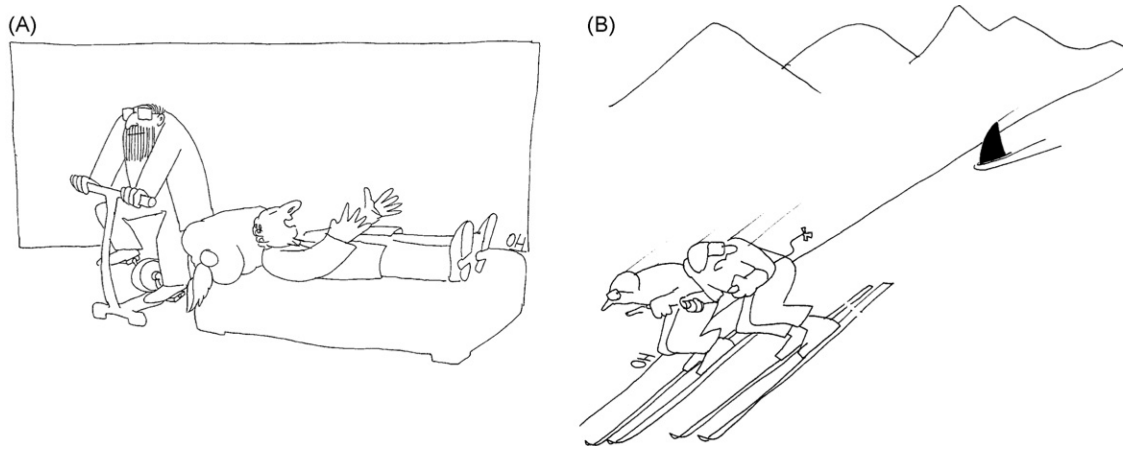

Fig. 1. Stimulus examples for an incongruity-resolution cartoon (A) and for a nonsense cartoon (B). Cartoons by Oswald Huber.

ences of these two types of humor stimuli as well as the influence of personality characteristics are investigated in the present fMRI experiment.

Most cognitive humor theories claim that humorous stimuli are processed in steps, although they do not agree about the nature and number of these steps (Attardo, 1997; Coulson & Kutas, 2001; Shultz, 1976; Suls, 1972). But they all assume that the initial information activates stored expectations or a script. Further information leads to the detection of an incongruity, constituted by the relation of the first script to another. In order to understand the punch line of the joke (either verbal jokes or visual jokes, i.e., cartoons) the incongruity has to be at least partially resolved. According to Ruch and colleagues (e.g., Ruch, 1992; Ruch & Hehl, 2007) the resolvability of the incongruity is a structural characteristic of humorous stimuli that strongly influences the perceived funniness but also other reactions such as aversion. In fact, this characteristic explains more variance of the funniness ratings than the content of a joke. Thus, the authors showed that humorous stimuli can be categorized according to the resolvability of their incongruity: On the one extreme of a continuum, *incongruity-resolution jokes* contain an incongruity that is (almost) completely resolvable. The common element of these humorous stimuli is that in their processing the recipient first discovers an incongruity, which is then playfully resolvable upon reinterpretation of the information available in the joke or cartoon. Fig. 1A is an example of an incongruity-resolution cartoon: The incongruity lies in the circumstance that the patient does not know that the psychotherapist is exercising instead of listening carefully. The incongruity is resolved if the psychotherapeutic session is reinterpreted as so boring for the psychoanalyst that he engages in another activity. It is also a comment on the prejudiced assumption that psychotherapists merely pretend to be empathic. On the other end of the continuum are *humorous stimuli based on nonsense*, which also have a surprising or incongruous punch line. However, the punch line may provide no resolution at all, provide a very partial resolution (leaving an essential part of the incongruity unresolved), or actually create new absurdities or incongruities. Fig. 1B is a nonsense cartoon that we used in the present experiment: Two skiers are chased by a shark which seems to swim in the snow. The incongruity is only partially resolvable through the visual analogy of one visual element (the diagonal line) that designates a mountain in connection with the skiers and the sea with respect to the shark. It cannot be both, so this situation is actually impossible and has more residual incongruity than the incongruity-resolution example (in which the situation is unusual, but most likely possible). Several issues, such as why there is a shark on the slope, remain unanswered (residual incongruity).

The preference for incongruity-resolution or nonsense stimuli can be measured with the 3 WD ("3 Witz-Dimensionen") humor test (Ruch, 1992, 1995). Besides stimuli that require incongruity-resolution and nonsense processing, a third stimuli group consistently emerged as a factor in factorial analyses: those with sexual content (e.g., Ruch, 1992; Ruch & Hehl, 2007). As only formal or structural and not content-related aspects are of interest in this study, the preference for sexual content is not considered further.[1]

As already mentioned, personality traits, such as openness, conservativism or intolerance of ambiguity, were shown to influence humor processing and appreciation (see, for example, Forabosco & Ruch, 1994; Ruch, 1988; Ruch, Accoce, Ott, & Bariaud, 1991; Ruch & Hehl, 2007). One of the personality characteristics that appears to influence humor appreciation is experience seeking, one of the subscales of the sensation seeking scale (Zuckerman, 1994). Experience seeking involves a search for novel sensations, stimulation and experiences through the mind and senses, through art, travel, music, and the desire to live in an unconventional style (see Ruch & Zuckerman, 2001). There is evidence that experience seeking is closely related to the novelty and complexity of stimuli (Zuckerman, 1984; see also Ruch, 1992; Ruch & Hehl, 2007). Experience seekers are characterized as having a high need for mental stimulation related to the pursuit of unfamiliar and complex environmental stimuli. Biological and social factors shape sensation seeking (Zuckerman, 2006). People with higher scores in sensation seeking show a larger responsiveness of the brain to novel stimuli, coupled to much faster habituation of brain responses on repeated stimulation. The volume of the right hippocampus (and a tendency on the left side) was shown to correlate with experience seeking, which is suggested to play a central role for processing of novel stimuli (Martin et al., 2007). It is suggested that the hippocampus compares incoming information with stored memories in order to index if a stimulus or information is novel (e.g., Lisman & Grace, 2005, see Nyberg, 2005).

Humorous stimuli can be seen as complex stimuli, since novelty has to be processed in the way that an incongruity has to be detected and playfully resolved (e.g., Suls, 1972; Shultz, 1976).

[1] The stimuli presented in this study were not of sexual content either. Since it is known that humor with sexual content is perceived differently and personality characteristics influence how this type of humor is perceived, sexual cartoons were explicitly excluded already in the pre-examinations: "...[it was]...searched... 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..." (Samson et al., 2008, p. 129).

Individuals with higher scores in experience seeking were found to search for more situations that make them laugh and might even explore humorous stimuli more intensely (Deckers & Ruch, 1992) and were reported to perceive a variety of situations as being funnier and to display more overt expression to humor (Lourey & McLachlan, 2003). Some studies showed that high experience seekers prefer nonsense humorous stimuli, whereas for low experience seekers the pattern was reversed. Experience-seeking scores correlated positively with appreciation of nonsense stimuli and negatively with appreciation of incongruity-resolution (e.g., Ruch, 1988; Forabosco & Ruch, 1994).

Previous fMRI studies showed several neuronal structures that are part of the network which is involved in humor processing: areas in the temporal lobe (e.g., temporal pole, anterior superior temporal sulcus, aSTS, e.g., Mobbs, Greicius, Abdel-Azim, Menon, & Reiss, 2003; Mobbs, Hagan, Azim, Menon, & Reiss, 2005; Moran, Wig, Adams, Janata, & Kelley, 2004; Wild et al., 2006) were associated with earlier steps of humor processing, such as the set-up of the joke for bringing stored expectations online. The following areas are substantially involved in cognitive humor processing, i.e., the comprehension process or incongruity-resolution, and are of particular interest in this study: the inferior frontal gyrus (IFG; see Bartolo, Benuzzi, Nocetti, Baraldi, & Nichelli, 2006; Goel & Dolan, 2001; Mobbs et al., 2003; Wild et al., 2006) and the temporal parietal junction (TPJ, e.g., Samson, Zysset, & Huber, 2008; Wild et al., 2006). The role of prefrontal areas is not yet clear, as they showed activation only in some of the existing studies (e.g., Wild et al., 2006). The ventro medial prefrontal cortex (vmPFC) as well as subcortical areas, i.e., the nucleus accumbens, were associated with humor appreciation, i.e., the affective aspect of humor processing (e.g., Goel & Dolan, 2001, 2007).

Despite the growing number of fMRI studies on neural correlates of humor processing only a small number of them took formal or structural aspects of the humorous stimuli into account: Goel and Dolan (2001) showed that the processing of phonological puns and semantic jokes evoked different brain activation patterns. In another study, Watson, Matthews, and Allman (2006) used verbal and visual material to show that humor processing is dependent on these modalities. Samson et al. (2008) demonstrated that different logical mechanisms are processed differently. The logical mechanism is the cognitive rule which determines *how* the incongruity of the joke has to be resolved in order to understand the punch line (e.g., one has to recognize that the punch line is based on role exchange; Attardo, Hempelmann, & DiMaio, 2002; Attardo & Raskin, 1991). In their study, the processing of three types of jokes differed according to their logical mechanisms—visual puns, semantic cartoons and Theory of Mind cartoons—and evoked different activation patterns. For example, visual puns provoked increased activation of the extrastriate cortex and Theory of Mind cartoons lead to increased activation of so-called mentalizing areas such as the anterior medial prefrontal cortex (amPFC) and the TPJ. Semantic cartoons did not differ from the network known to be involved in the incongruity-resolution process (i.e., IFG and TPJ). Other studies also showed differences in the processing of Theory of Mind cartoons vs. cartoons for which it is not necessary to attribute mental states to joke characters in order to get the joke (Gallagher et al., 2000; Marjoram et al., 2006).

Up to now, only one brain imaging study investigated personality differences in humor processing: Mobbs et al. (2005) found the right orbital frontal cortex, the ventro lateral prefrontal cortex and bilateral temporal cortices to correlate with extraversion, whereas introversion correlated with several regions, particularly with the amygdala. Emotional stability (i.e., the inverse of neuroticism) correlated with increased activation in the mesocortical–mesolimbic reward circuitry, whereas a humor questionnaire was not associated with an increase or decrease in brain activation. Extraversion was shown to be associated with positive emotional experience (e.g., Costa & McCrae, 1980, 1991) and Canli et al. (2001; see also Canli, 2006) showed greater brain reactivity of extraverts to positive stimuli.

The aim of the present study is twofold. First, it focuses on the resolvability of the incongruity in non-verbal cartoons as a structural characteristic that influences cognitive components of humor processing that, in turn, might lead to different neuronal activation patterns. It contrasts the two assumed extremes on this dimension of resolvability: incongruity-resolution and nonsense stimuli. In a recently published study, Samson et al. (2008) showed that humorous cartoons activated the vmPFC, the left IFG, TPJ and supramarginal gyrus bilaterally. Because the latter three regions in particular are involved in the incongruity-resolution process, we assumed to find differences in their activation for incongruity-resolution and nonsense jokes. In particular, we expected to find these areas to be more strongly activated in the processing of incongruity-resolution stimuli because more incongruity-resolution is possible, i.e., more sense can be made and more explanation and integration of information is feasible. We assume, on the other hand, that as a result of processing of nonsense humor stimuli people laugh about the absurdity of the two (almost) incompatible scripts rather than about the result of a playful and successful incongruity-resolution process.

The second aim of this study is to investigate the influence of individual experience-seeking scores on humor processing in general (i.e., humorous stimuli vs. non-funny pictures containing an irresolvable incongruity). Humorous stimuli can be meaningfully investigated in relation to the neural response and individual experience-seeking scores because they can be seen as complex stimuli containing novel elements (such as the incongruity) which might be more attractive to explore for high experience seekers. As extraversion was shown to be associated with increased brain activation in humor processing (Mobbs et al., 2005) and extraversion (particularly the subscale excitement-seeking) is known to correlate with experience seeking (e.g., Aluja, García, & García, 2003) we expect increased brain activations in individuals with higher experience-seeking scores. Furthermore, the experience-seeking scores shall be analyzed in relation to the neural correlates of the processing of nonsense vs. incongruity-resolution cartoons, as experience seekers were shown to prefer humorous stimuli based on nonsense over stimuli based on incongruity-resolution (e.g., Forabosco & Ruch, 1994). The question here is whether experience seekers demonstrate a different pattern of activation for types of humor that they usually prefer or dislike. Finally, the preference for incongruity-resolution or nonsense humorous stimuli was measured with the 3 WD (Ruch, 1992, 1995). Whether the preference for one over the other type of humor influences the neural response during humor processing will be analyzed as well.

2. Method

2.1. Subjects

Seventeen neurologically healthy and right-handed subjects (nine female, eight male, mean age 26.06, years, S.D. = 3.25) participated in this study. Written informed consent from all subjects was obtained prior to the scanning session. All subjects had normal or corrected-to-normal vision and were native German speakers. None of the subjects was on 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.

2.2. Stimuli

The data reported in this paper originate from the same experiment as reported in Samson et al. (2008). For the first analysis of incongruity-resolution and nonsense humorous stimuli, only a part of the 90 presented humorous stimuli were considered (see below). For the influence of personality characteristics on humor processing, humorous cartoons with varying degrees of resolvability were first contrasted to a non-funny control condition (INC, these cartoon-like pictures contained irresolvable incongruities), then, nonsense cartoons were contrasted to incongruity-resolution cartoons. For a more detailed account of stimuli and design, see Samson et al. (2008).

In the study by Samson et al. (2008), three different types of cartoons that differ regarding their logical mechanism were presented. As these three types showed differences in brain activation, it was important for the present analysis to have them equally distributed over incongruity-resolution and nonsense humorous stimuli. In order to categorize the 90 cartoons into the groups of incongruity-resolution and nonsense stimuli, they were rated by 19 subjects (10 male, 9 female, mean age 26.89, S.D. = 5.12) for grotesqueness, subtleness and residual incongruity, as these ratings differentiated between incongruity-resolution and nonsense humorous stimuli: nonsense jokes, for example, are perceived to be more grotesque and subtle (Samson & Ruch, 2005) and evoking more residual incongruity (Hempelmann & Ruch, 2005). A 2 means cluster analysis (with max. 10 iterations) for the 90 cartoons used in the fMRI experiment revealed two clusters with $N = 32$ and $N = 58$ cartoons. The final cluster centers are for grotesque (cluster1: 3.30; cluster2: 2.74; $F(1, 88) = 25.322$, $p < .001$), for subtleness (cluster1: 1.80; cluster2: 2.41; $F(1, 88) = 30.137$, $p < .001$) and for residual incongruity (cluster1: 1.92; cluster2: .90; $F(1, 88) = 107.557$, $p < .001$).

Because nonsense humorous stimuli are known to have low values in subtleness and high values on grotesqueness and residual incongruity, cluster1 can be described as nonsense stimuli ($N = 32$), whereas cluster2 can be described as incongruity-resolution stimuli ($N = 58$). The results from the cluster analysis were verified with a canonical discriminant analysis. The canonical discriminant function yielded an Eigenvalue of 1.984, a canonical correlation of .815, Wilks' Lambda .335, $\chi^2(3) = 94.580$, $p < .001$. Only one cartoon was not correctly classified and was excluded for further analyses.

In a next step 30 cartoons for each condition were selected (see Fig. 1 for examples): With the aim not to confound the groups of incongruity-resolution and nonsense stimuli and the three types of logical mechanisms (visual puns, semantic cartoons, Theory of Mind cartoons), the three logical mechanisms were to be equally distributed among the two groups of incongruity-resolution and nonsense humor. For this, first, the number of cartoons per group was determined. As there were only seven semantic and seven Theory of Mind cartoons in the group of nonsense humorous stimuli, all of these had to be selected. Therefore, approximately the same number of semantic cartoons and Theory of Mind cartoons, respectively, which were categorized to be incongruity-resolution had to be randomly selected for this group.

The visual puns were selected according to high grotesqueness and low subtleness ratings, as well as high residual incongruity ratings for the nonsense group. The criteria were reversed for the incongruity-resolution group. Finally, the nonsense group consisted of 15 visual puns, 8 semantic cartoons and 7 Theory of Mind cartoons. The incongruity-resolution group consisted of 13 visual puns, 9 semantic cartoons and 8 Theory of mind cartoons. Thus, the logical mechanisms were equally distributed over incongruity-resolution and nonsense cartoons ($\chi^2(2) = .268$, $p = .874$).

Table 1 summarizes the ratings of grotesqueness, subtleness and residual incongruity for the selected incongruity-resolution and nonsense cartoons and shows that for all three ratings, the two stimuli groups differ significantly, as one-way ANOVAs revealed.

2.3. Personality measures

The *Sensation Seeking Scale* (Zuckerman, 1994) consists of four different subscales and a total score. Here, only the subscale experience seeking was of interest. Experience seeking is characterized by a search for novel sensations and experiences through the mind and senses, in several domains and the desire to live in an unconventional style.

The *3 WD ("3 Witz-Dimensionen") humor test* (Ruch, 1992, 1995) was designed to assess appreciation of jokes and cartoons of the three humor categories that were labelled incongruity-resolution, nonsense, and sexual humor. They contain 50 jokes and cartoons, which are rated on funniness and aversiveness using two 7-point scales. Here, only the funniness ratings of incongruity-resolution (INC-RES) or nonsense (NON) humorous stimuli were of interest, as well as the relative preference for humorous stimuli based on nonsense over incongruity-resolution, i.e., the Structure Preference Index (SPI; obtained by subtracting INC-RES from NON).

Table 1
Means and standard deviations of the ratings for the two stimuli groups (30 stimuli in each condition).

	Incongruity-resolution cartoons Mean (S.D.)	Nonsense cartoons Mean (S.D.)
Grotesqueness[a]	2.73 (.44)	3.25 (.52)
Subtleness	2.47 (.48)	1.92 (.51)
Residual incongruity	.98 (.43)	1.78 (.43)

Nonsense cartoons are perceived to be more grotesque, less subtle and having more residual incongruity.

[a] One-way ANOVAs yielded significant differences between the two stimuli conditions for grotesqueness ($F(1, 57) = 16.774$, $p < .001$), subtleness ($F(1, 57) = 15.141$, $p < .001$) and residual incongruity ($F(1, 57) = 51.167$, $p < .001$).

2.4. Task paradigms

By pressing a button the participants had to indicate whether they understood the joke in the cartoon or not, while recognition time was measured. This procedure allowed for the distinction between cartoons that were understood but not considered funny and cartoons that were not understood and therefore not funny. Cartoons that were not understood were excluded from 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 s. 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 need not 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 a total of 180 trials (90 humorous stimuli, 30 control pictures containing irresolvable incongruities, 30 BAS and 30 null-events were presented). Trials were presented every 10 s on average and with variable stimulus-onset delays (0, 400, 800, 1200 or 1600 ms). The experiment lasted a total of 30 min. 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 humorous stimuli on a scale from 0 = not funny at all to 6 = very funny. Furthermore, the participants were asked to fill in the Sensation Seeking Scale (Zuckerman, 1994) and the 3 WD (Ruch, 1992).

2.5. MRI scanning procedure

The experiment was carried out on a 3T scanner (Siemens TRIO, Erlangen, Germany) at the Max-Planck-Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.

For the cognitive paradigm, 26 axial slices (3 mm × 3 mm × 3 mm resolution, .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.

2.6. fMRI data analysis

The fMRI data was 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 was 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 highpass 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 (three rotational, three 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 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; Worsley & Friston, 1995; Zarahn, Aguirre, & d'Esposito, 1997). The design matrix was generated with a box-car function with reaction time as onset, 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 11 or more continuous voxels (Braver & Bongiolatti, 2002; Forman et al., 1995).

Furthermore, the individual contrast images were used for a random-effects second-level analysis with an additional regressor coding the experience-seeking scores or the SPI, respectively. To protect against false positive activations, only regions with a Z-score greater than 2.58 ($p < .005$, uncorrected) and with a volume greater than 297 mm^3 (11 voxels) were considered (Braver & Bongiolatti, 2002; Forman et al., 1995).

Finally, a time course analysis of the fMRI signal was calculated. Trial-averaged time courses (stimulus onset locked) were obtained on a voxel-by-voxel basis for each subject at a sampling rate of .2 s for the incongruity-resolution cartoons as well as for the nonsense cartoons. The mean signal intensity of the entire time course was taken as baseline for the calculation of the percent signal change. The time course of the null events was subtracted from the time course of the two task conditions (Burdock, Buckner, Woldorff, Rosen, & Dale, 1998). Further, the maximum percent signal change was extracted for each subject and condition.

3. Results

3.1. Behavioral data

The behavioral data showed that incongruity-resolution cartoons were better understood than nonsense cartoons, which was revealed by a paired sample t-test ($t(16) = 3.011$, $p < .01$). However, the two stimuli groups did not differ regarding recognition time and funniness ratings. See Table 2 for descriptive statistics.

Experience-seeking scores had a mean of 6.94 (S.D. = 1.50). The SPI had a mean of −3.18 (S.D. = 6.57). There was no effect of gender on the experience-seeking scores or the SPI. The participants did not significantly prefer incongruity-resolution over nonsense cartoons, as measured with the 3 WD. In previous studies experience seeking was shown to correlate positively with funniness ratings of nonsense and negatively of incongruity-resolution humorous stimuli, measured with the 3 WD (Ruch, 1992). However, with these 17 subjects, no significant correlations were found between experience seeking and incongruity-resolution or nonsense stim-

Table 2
Means and standard deviations for comprehensibility (0 = not understood, 1 = understood), recognition time (in seconds), and funniness ratings (from 0 = not funny at all, to 6 = very funny, $N = 17$) the two types of humorous stimuli.

	Incongruity-resolution cartoons Mean (S.D.)	Nonsense cartoons Mean (S.D.)
Comprehensibility[a]	.89 (.06)	.80 (.14)
Recognition time	4.67 (.73)	4.30 (.52)
Funniness	3.30 (.70)	3.51 (1.39)

[a] Incongruity-resolution cartoons were better understood than nonsense cartoons ($t(16) = 3.011$, $p < .01$).

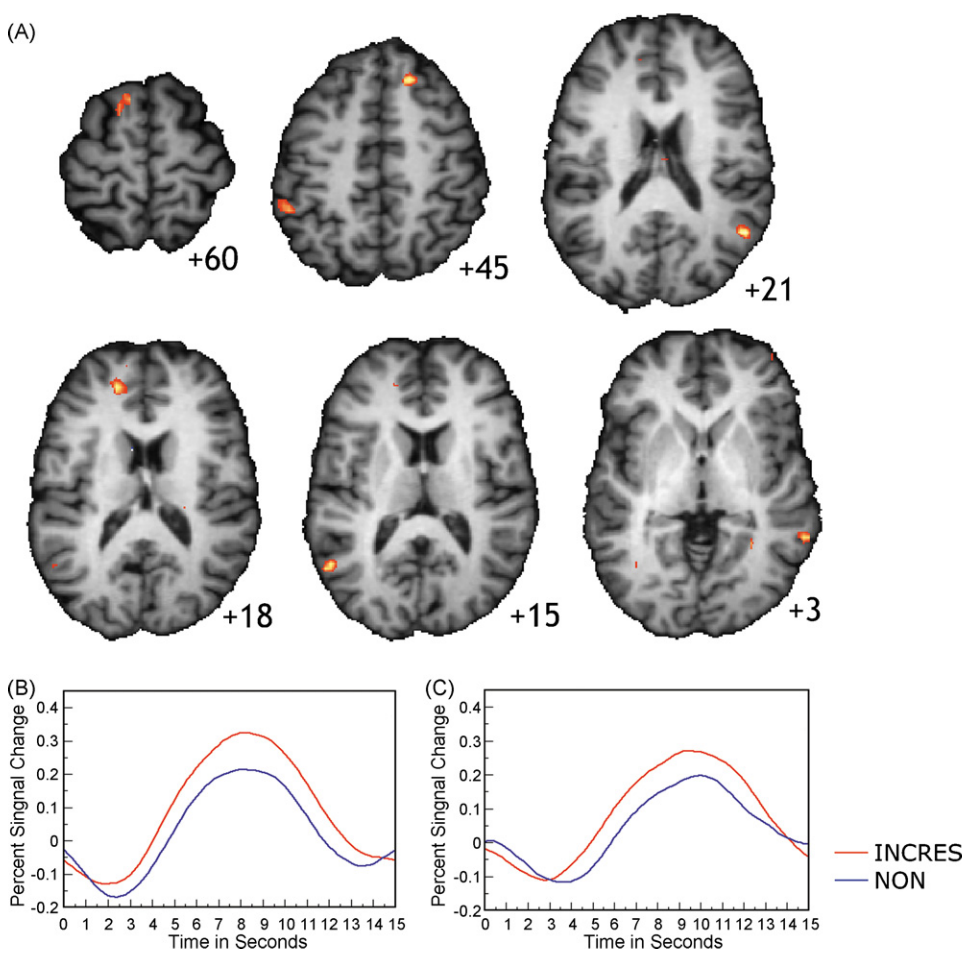

Fig. 2. (A) Main activations for incongruity-resolution cartoons vs. nonsense cartoons. Significant regions of activation are projected onto the cortical surface of an average brain, obtained by nonlinear transformation of the participants' individual anatomies. Axial views are shown. All maps are thresholded at $z > 3.09$, $p < .001$, uncorrected. Event-related hemodynamic response in (B) left TPJ and (C) right TPJ during processing of incongruity-resolution (INCRES) and nonsense (NON) cartoons. Presentation of stimuli occurred at 0 s.

Table 3
Main activations for incongruity-resolution cartoons vs. nonsense cartoons, $N = 17$; Brodman areas (BA), Talairach coordinates, volume and Z-maximum of the main activated regions.

Area	BA	Talairach coordinates			
Incongruity-resolution cartoons		*x*	*y*	*z*	Volume (*Z*-max)
R superior frontal gyrus (SFG)	8/9	13	32	42	594 (3.97)
L superior frontal gyrus (SFG)	8/9	−11	14	60	324 (3.47)
L anterior medial prefrontal cortes (amPFC)	10	−17	41	18	405 (3.78)
L angular gyrus	39/7	−53	−46	45	405 (3.45)
L temporo-parietal junction (TPJ)	39	−53	−61	15	324 (3.69)
R temporo-parietal junction (TPJ)	39	49	−58	21	621 (3.91)
R posterior middle temporal gyrus (pMTG)	37	58	−49	3	297 (3.64)

The volume is reported in mm^3 and z-values were thresholded at $z < 3.09$. Reported clusters contain at least 11 (297 mm^3) continuous voxels.

uli, measured neither with the 3 WD nor with the stimuli used in the present study, as well as no correlation with the SPI. Further analysis revealed that only the incongruity-resolution cartoons of our experiment correlated positively with the incongruity-resolution stimuli of the 3 WD ($r(17) = .503$, $p < .05$). The lack of significant correlations might be due to the limited number of subjects and the fact that they did not clearly prefer one type of humor over the other.

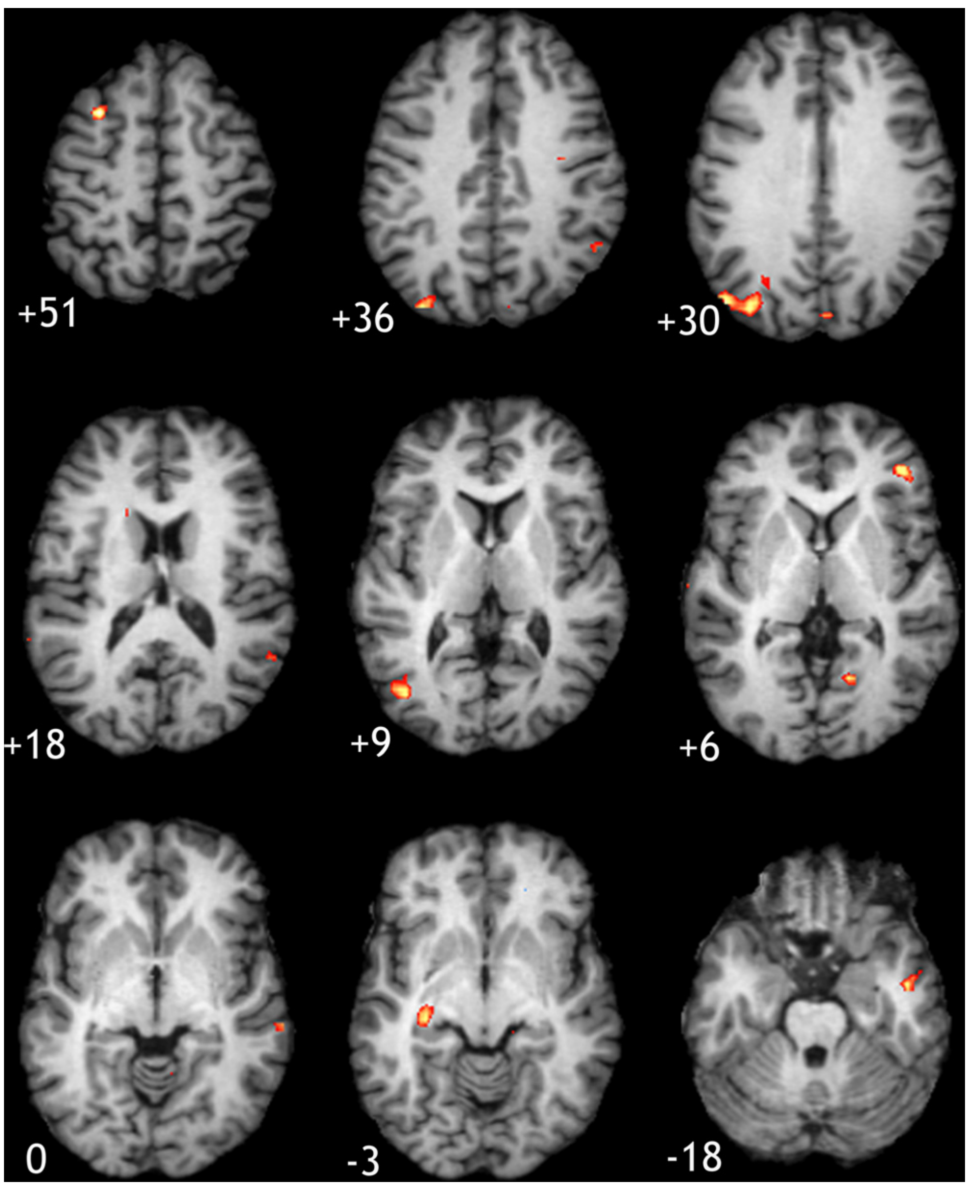

Fig. 3. Humor processing in relation to experience seeking: main activations funny cartoons vs. control condition (irresolvable incongruities). Significant regions of activation are projected onto the cortical surface of an average brain, obtained by nonlinear transformation of the participants' individual anatomies. Axial views are shown. All maps are thresholded at $z > 2.58$, $p < .005$, uncorrected.

Table 4
Humor processing in relation to experience seeking: main activations for funny cartoons vs. control condition (irresolvable incongruities), $N = 17$; Brodman areas (BA), Talairach coordinates, volume and Z-maximum of the main activated regions.

AREA	BA	Talairach coordinates			
Funny cartoons		x	y	z	Volume (Z-max)
L middle frontal gyrus (MFG)	6/8	−29	11	51	486 (3.90)
R inferior frontal gyrus (IFG)	9	40	35	6	486 (3.34)
R anterior superior temporal sulcus (aSTS)	21	43	−10	−18	864 (3.34)
R posterior superior temporal sulcus (pSTS)	21	61	−31	0	324 (3.04)
R temporo-parietal junction (TPJ)	22/39	52	−55	18	405 (2.80)
R angular gyrus	40	49	−58	36	459 (2.83)
L inferior parietal lobe	39/40	−47	−79	30	4212 (3.51)
L occipital gyri	37/19	−41	−76	9	1080 (3.36)
R medial occipitotemporal gyrus	37/19	13	−64	6	1107 (3.25)
L hippocampus		−29	−28	−3	405 (3.32)

The volume is reported in mm^3 and z-values were thresholded at $z < 2.58$. Reported clusters contain at least 11 (297 mm^3) continuous voxels.

3.2. Imaging results

3.2.1. Comparison of incongruity-resolution vs. nonsense cartoons

In order to analyze which brain structures react to the degree of resolvability of the incongruity, incongruity-resolution cartoons (incongruity is almost completely resolvable) were contrasted to nonsense cartoons (incongruity not completely resolvable, high degree in residual incongruity). Only the understood cartoons entered the analysis. This comparison revealed significant activations for incongruity-resolution jokes, but no specific areas for nonsense jokes: The superior frontal gyrus (SFG) bilaterally, amPFC and several activations around the left and right temporo-parietal junction (left angular gyrus, temporo-parietal junction bilaterally and right posterior middle temporal gyrus, pMTG) were more strongly involved in processing of incongruity-resolution cartoons.

Fig. 2A shows the resulting activation maps for incongruity-resolution vs. nonsense cartoons and Table 3 reports the coordinates, volumes and maximum z-values from the group averaged data. Fig. 2B shows the underlying haemodynamic response in the left and right TPJ during processing of incongruity-resolution and nonsense cartoons.

3.2.2. Experience seeking and humor processing

Higher experience-seeking scores correlated positively with brain activation during humor processing in the following areas: the left middle frontal gyrus (MFG) and the right IFG in the frontal cortex, and small activations in the right aSTS and pSTS/TPJ and angular gyrus, left inferior parietal lobe and occipital gyri. Furthermore, the right medial occipitotemporal gyrus and left hippocampus showed stronger activation corresponding to experience-seeking scores.

Fig. 3 shows the resulting activation maps for funny cartoons vs. pictures containing an irresolvable incongruity in relation to the individual experience-seeking scores and Table 4 reports the coordinates, volumes and maximum z-values from the group averaged data. Fig. 4 shows the correlation of experience-seeking scores with activation in the hippocampus.

3.2.3. Comparison of nonsense vs. incongruity-resolution and experience seeking

The left anterior IFG, inferior frontal junction (IFJ) and right IFG, as well as in the extrastriate cortex showed different activations in processing of nonsense vs. incongruity-resolution cartoons in relation to experience seeking.

Fig. 5A shows the resulting activation maps for nonsense vs. incongruity-resolution cartoons in relation to individual experience-seeking scores and Table 5 reports the coordinates, volumes and maximum z-values from the group averaged data. Fig. 5B shows the correlation with experience-seeking scores in the left IFJ.

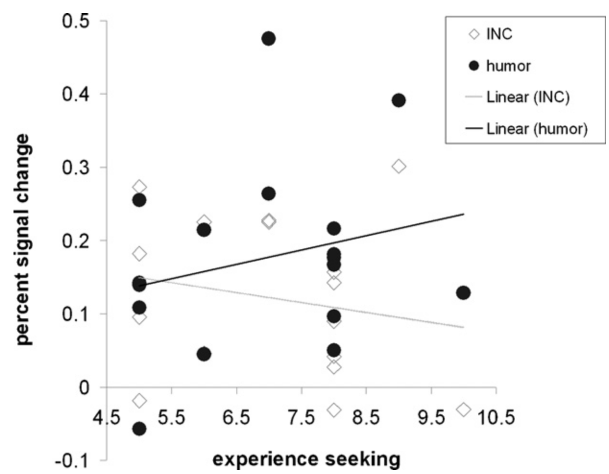

Fig. 4. Percent signal change in relation to experience seeking for humor processing and the control condition (irresolvable incongruities = INC) in the left hippocampus (−29 −28 −3).

3.2.4. The influence of the structural preference index (SPI)

The relative preference for nonsense over incongruity-resolution humorous stimuli (SPI, measured with the 3 WD) showed no significant activations neither in humor processing in general nor in nonsense vs. incongruity-resolution.

4. Discussion

The first aim of this study was to investigate differences in the processing of incongruity-resolution and nonsense cartoons that differ with respect to the resolvability of their incongruity: Whereas in incongruity-resolution cartoons the incongruity of the joke can be almost completely resolved, nonsensical humorous stimuli are characterized by high residual incongruity of the joke (Hempelmann & Ruch, 2005), which cannot be resolved (completely), while new incongruities may even emerge in the attempt to resolve the main incongruity. Our results show that processing of incongruity-resolution cartoons, in contrast to nonsense cartoons, leads to more activation in areas around the TPJ bilaterally, the SFG bilaterally and the right amPFC. On the other hand, no specific activation was found for processing of nonsensical humorous stimuli.

As the TJP was also found to be involved in the incongruity-resolution process in funny cartoons but not in non-funny pictures containing an irresolvable incongruity (Samson et al., 2008), we

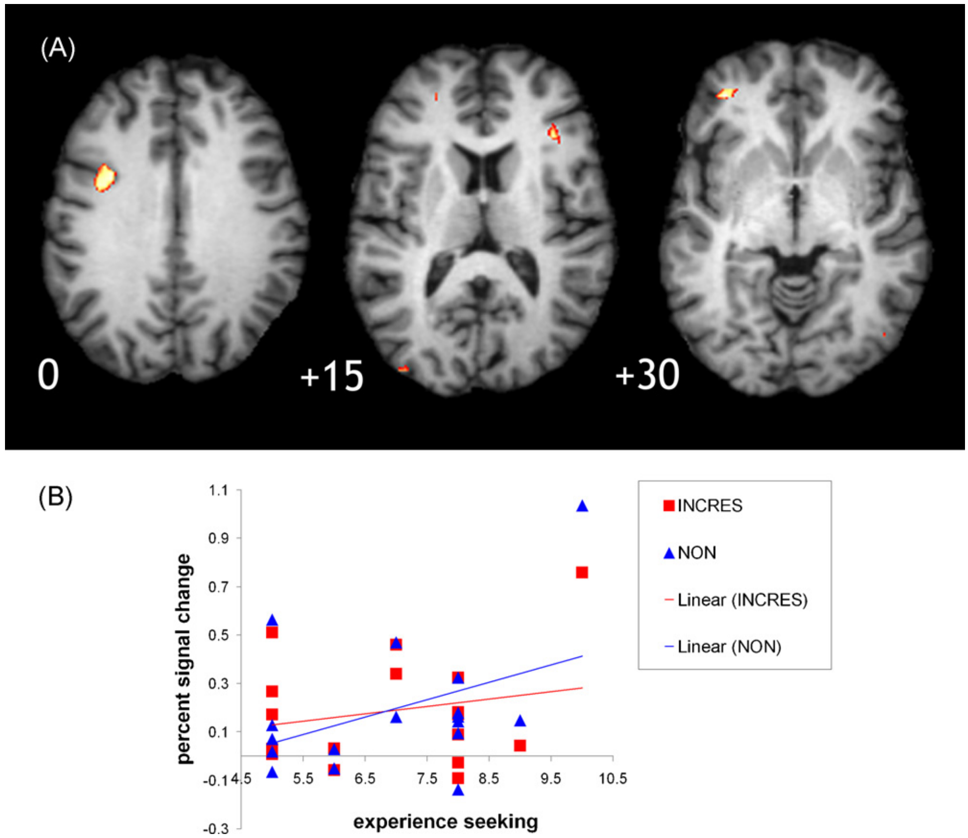

Fig. 5. (A) Main activations nonsense (=NON) vs. incongruity-resolution (=INCRES) cartoons in relation to individual experience-seeking scores; significant regions of activation are projected onto the cortical surface of an average brain, obtained by nonlinear transformation of the participants' individual anatomies. Axial views are shown. All maps are thresholded at $z > 2.58$, $p < .005$, uncorrected. (B) Percent signal change in relation to experience seeking for processing of nonsense and incongruity-resolution cartoons in the left inferior frontal junction (−32 2 30).

claim that this area is relevant for the resolution of the incongruity: the more information can be integrated and the more sense a joke makes (as incongruity-resolution cartoons do), the more activation can be found in the TPJ. This is in line with interpretations of the TPJ as involved in integration of multi-sensory information and coherence building (see Ferstl & von Cramon, 2002) and inferring knowledge (Goel, Grafman, & Hallett, 1995), as well as a multimodal convergence zone with connections to the limbic system (Barnes & Pandya, 1992). In a meta-analysis, Decety & Lamm (2007) recently showed that this area is activated not only during high-level social-cognitive processes but also in lower-level computational processes, such as attention orientation. Therefore, the TPJ may contribute to generating, testing and correcting internal predictions about external sensory events, which is crucial for the resolution of incongruity in humor processing. In nonsense cartoons, the search for a possibility to resolve the incongruity will still be initiated, but less information can be integrated (since often only a partial resolution is possible, which generates more residual incongruity). However, the mere *search* for a possibility to resolve the incongruity does not lead to more activation in the TPJ.

With an increase of incongruity that can be resolved, also more activation is found in the SFG bilaterally. One study showed that a patient laughed when the SFG was stimulated. The patient gave different explanations for the laughter each time, attributing it to any element or object she was presented with (Fried, Wilson, MacDonald, & Behnke, 1998). It might be possible that the SFG is therefore involved in (attempting to) "making sense" or "attribution". Furthermore, this area is also involved in higher processes described under the concepts of monitoring and manipulation, executive processing and is thought to contribute to higher cognitive functions and particularly to working memory (see, for example, Owen, 2000; Petrides, 2000). As the SFG was shown to be involved in higher levels of working memory processing (monitoring and manipulation) and to react to an increase in

Table 5
Nonsense vs. incongruity-resolution cartoons in relation to experience seeking: main activations, $N = 17$; Brodman areas (BA), Talairach coordinates, volume and Z-maximum of the main activated regions.

AREA	BA	Talairach coordinates			
Nonsense cartoons		*x*	*y*	*z*	Volume (*Z*-max)
L anterior inferior frontal gyrus (IFG)	46	−35	41	0	324 (3.06)
L inferior frontal junction (IFJ)	44/6	−32	2	30	1026 (3.00)
R inferior frontal gyrus (IFG)	44	34	23	15	621 (2.92)
L extrastriate cortex/occipital gyri	37/19	−38	−91	15	324 (2.70)

The volume is reported in mm^3 and z-values were thresholded at $z < 2.58$. Reported clusters contain at least 11 (297 mm^3) continuous voxels.

executive demand (Du Boisgueheneuc et al., 2006), we claim that management or integration of concurrent information in incongruity-resolution cartoons needs more executive processing than in nonsense cartoons. Probably, humorous stimuli based on incongruity-resolution require more mental manipulation of information and mental organization. Furthermore, the processing of incongruity-resolution stimuli provokes more activation in the amPFC than processing of nonsense cartoons.[2] It is possible that in nonsense cartoons less self-referential mental activity can be established (e.g., Gusnard, Akbudak, Shulman, & Raichle, 2001; Zysset, Huber, Samson, Ferstl, & von Cramon, 2003) as this type of humor is known to be more absurd and grotesque (see Samson & Ruch, 2005) and therefore less reference to reality or to one's own experiences might be required. In addition, humorous stimuli based on incongruity-resolution were described to be more open for interpretation (Ruch, 1981), which might facilitate more self-referentiality.

Although the IFG is shown to be involved in cognitive humor processing (e.g., Goel & Dolan, 2001; Mobbs et al., 2003; Moran et al., 2004; Samson et al., 2008; Wild et al., 2006), it does not seem to react to the degree of the resolvability of the incongruity. Therefore, it might be involved in processes that are required for processing of humorous stimuli based on either incongruity-resolution or nonsense.

One very interesting question is why processing of nonsense jokes does not evoke the same activation pattern as non-funny pictures containing an irresolvable incongruity. These pictures evoked activation, for example, in the rostral cingulate zone (BA 8), indicating conflict monitoring or error processing (Samson et al., 2008), presumably since the incongruities were not resolvable or made no sense at all. However, that nonsense cartoons were perceived to be different from pictures containing irresolvable incongruities can also be seen in the ratings: In contrast to the control condition, nonsense cartoons were rated to be understood and perceived to be funny. That is, unresolved incongruity that is understood as humorous is different from non-humorous unresolved incongruity.

Why do incongruity-resolution cartoons require more involvement of the TPJ and prefrontal areas? In humor processing in general, an incongruity first has to be detected and then, in a process similar to problem-solving, a cognitive rule has to be found that resolves the incongruity in order for the joke to make—at least partial—sense. Ruch (1981) defined incongruity-resolution jokes as open for interpretations, offering more possibilities to explain the punch line than humorous stimuli based on nonsense. As there are more possibilities to explain the punch line of the joke in incongruity-resolution than in nonsense jokes subjects have to continuously generate new hypotheses about the relation of the incongruity. In the comprehension process, alternative interpretations are considered, until one explanation makes sense in a funny way. This probably requires more mental manipulation and organization (working memory) and more integration of information than in nonsense jokes, because in humorous stimuli based on nonsense something unexpected, impossible, or absurd happens and, often, the incongruities are not resolvable. Thus subjects do not even try. For example, since things happen that are technically or otherwise impossible (e.g., a shark swimming in the snow), no explanation of the incongruity is required. The appreciation of these kinds of jokes emerges rather from a play with thoughts and with imagination. The perceiver enjoys absurd, complex incongruities that are not or only partially resolvable. Therefore, one might say that incongruity-resolution cartoons make more sense and are more easily explained.

The second aim of the study was to investigate the influence of inter-individual differences in experience seeking on neural correlates of humor processing: Experience seeking was positively correlated, inter alia, with humor processing in the left IFG, MFG and activations around the bilateral TPJ. As experience seekers tend to engage in investigatory behaviors such as exploring unknown locations, trying new food, etc., it is conceivable that they prefer to explore stimuli that require more cognitive processing to be found humorous: The cartoons are possibly more intensely searched for funny elements. Due to the more intense exploration of humorous stimuli high experience seekers might be more capable to make sense of the incongruities contained in the cartoons. Already Watson et al. (2006) showed the MFG to be involved in visual imagery related to humor processing. Furthermore, experience seekers show more activation in the hippocampus during humor processing. This area was shown to play a central role in processing novel stimuli (e.g., Legault & Wise, 2001, see Nyberg, 2005). The hippocampus is capable of comparing incoming information with stored memories in order to index whether that information is novel (Lisman & Grace, 2005). An observed relationship between experience seeking and hippocampal volume reflects either an association between this volume and the tendency to pursue novelty, or a more general tendency to pursue any form of mental stimulation (e.g., any form of sensation seeking, Martin et al., 2007). As the experience-seeking scale (Zuckerman, 1994) measures the tendency to pursue novel behavioral and cognitive experiences, we interpret the hippocampus activation to be involved in processing the novelty of humorous stimuli (i.e., incongruities, but also the result of an incongruity-resolution process), which is more pronounced in experience seekers.

Furthermore, it was analyzed whether individuals with different scores on the experience-seeking scale react differently to incongruity-resolution and nonsense cartoons. Although incongruity-resolution provokes more activation of the amPFC, SFG bilaterally, left angular gyrus, TPJ bilaterally and right pMTG than nonsense cartoons—if no individual differences are taken into account—more brain reactivity was found in the processing of nonsense than in incongruity-resolution cartoons in individuals with higher experience-seeking scores: More activation around the bilateral IFG and left extrastriate cortex was found. This is in line with the above-mentioned interpretation of the activations found in relation to humor processing: obviously, experience seekers tend to process nonsense cartoons semantically deeper and explore them more intensely. Although not reflected in the behavioral data within these 17 subjects, interestingly, high sensation seekers show more activation during processing of nonsense cartoons, for example in the left IFJ. The pattern seems to be reversed in low experience seekers. This is in line with previous findings that experience seekers prefer nonsense over incongruity-resolution (e.g., Ruch, 1988; Forabosco & Ruch, 1994). That experience seeking alters the neural humor response is a promising result. However, further studies are needed to confirm the relation between experience seeking and its neural correlates during processing of humorous stimuli based on incongruity-resolution and nonsense.

In our study, experience-seeking scores did not correlate significantly with funniness ratings. This might be due to the limited number of participants. However, other possibilities for interpretation should be considered: As two studies showed that sensation seekers tend to portray smiles and laughter more often and per-

[2] Samson et al. (2008) found the amPFC to be involved in Theory of Mind cartoons, but not in visual puns, semantic cartoons or in humor processing in general. The same amount of Theory of Mind cartoons was found among the incongruity-resolution and nonsense cartoons. Thus, the amPFC activation found in the present study has more likely to do with self-referential processes than with attributing mental states to others. According to Frith and Frith (1999) (see Frith and Frith, 2003, for a review) the mPFC is engaged when we attend to our own mental states as well as those of others.

ceive more events as being funnier (this was measured with humor self-report questionnaires, see Deckers & Ruch, 1992; Lourey & McLachlan, 2003), it is possible that they search more intensely for funny events. But it is also possible that the same stimulus is rated the same by high and low experience seekers (as in the present study): due to constant underarousal, experience seekers have to explore stimuli more deeply in order to appreciate them to the same degree as low experience seekers. It is also conceivable that high experience seekers require more intense stimulation to reach an optimal level of arousal (see also Zuckerman, 2006). Furthermore, it remains unclear why in our study experience seeking did not correlate with the relative preference for humorous stimuli based on nonsense over incongruity-resolution as it did in the study by Forabosco and Ruch (1994) who found even a negative correlation between experience seeking and appreciation of incongruity-resolution stimuli. Possibly, the individual differences are too subtle to be investigated with only 17 subjects with varying scores of experience seeking. Further studies have to be run, for example with participants with extreme scores on experience seeking who also differ in their preference for humorous stimuli based on nonsense and incongruity-resolution. Investigating individuals with more extreme scores on the SPI might also evoke neural correlates during humor processing for individuals who clearly prefer incongruity-resolution or nonsense humorous stimuli.

In conclusion, the neuronal data of our study supports that humorous stimuli based on incongruity-resolution and nonsense are processed differently: The circumstance that in incongruity-resolution cartoons more information can be integrated and more sense can be established leads to higher activation in the TPJ, the manipulation of this information (scripts) leads to more activation of the SFG and closer reference to reality leads to more activation of the amPFC. In nonsense humorous stimuli, on the other hand, people laugh more about the absurdity of rather incompatible scripts. This corresponds to less activation in frontal and temporo-parietal regions. Furthermore, the TPJ is confirmed to be involved in the incongruity-resolution process, and not in the *detection* of incongruity in humor, as some of the previous studies have claimed (e.g., Moran et al., 2004). Experience seeking seems to be a personality characteristic that influences the neural correlates of humor processing. Experience seeking correlates positively with activation in areas that are involved in humor processing (i.e., IFG, TPJ), but also with activation in the hippocampus. High experience seekers seem to process complex and novel stimuli—one type being humorous stimuli—more deeply and explore them more intensely than low sensation seekers.

Whenever new imaging studies unravel the cognitive and affective neural correlates of humor processing, further questions arise in turn: For example, nonsense jokes seem to consist of three different groups: those that are not resolvable, are only partially resolvable and those in which new incongruities are introduced for the resolution of the main incongruity (e.g., Ruch & Hehl, 2007). Altogether, these three subgroups of nonsense-based humorous stimuli have in common that they show more residual incongruity and that less incongruity-resolution is possible. In further studies, these three subgroups might be differentiated in more detail. Further studies might also concentrate more on affective aspects of humor processing or integrate a social partner in order to investigate for example the moderating effects of the use of humor in social interaction.

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