Cerebral Cortex February 2007;17:314-324
doi:10.1093/cercor/bhj149
Advance Access publication March 2, 2006

Brain Activation during Sight Gags and Language-Dependent Humor

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Humor is a hallmark of human discourse. People use it to relieve stress and to facilitate social bonding, as well as for pure enjoyment in the absence of any apparent adaptive value. Although recent studies have revealed that humor acts as an intrinsic reward, which explains why people actively seek to experience and create humor, few have addressed the cognitive aspects of humor. We used event-related functional magnetic resonance imaging to differentiate brain activity induced by the hedonic similarities and cognitive differences inherent in 2 kinds of humor: visual humor (sight gags) and language-based humor. Our findings indicate that the brain networks recruited during a humorous experience differ according to the type of humor being processed, with high-level visual areas activated during visual humor and classic language areas activated during language-dependent humor. Our results additionally highlight a common network activated by both types of humor that includes the amygdalar and midbrain regions, which presumably reflect the euphoric component of humor. Furthermore, we found that humor activates anterior cingulate cortex and frontoinsular cortex, 2 regions in the brain that are known to have phylogenetically recent neuronal circuitry. These results suggest that humor may have coevolved with another cognitive specialization of the great apes and humans: the ability to navigate through a shifting and complex social space.

Keywords: anterior cingulate, cartoons, evolution, fMRI, frontoinsula, jokes

Introduction

The phenomenon of humor is universal among humans (Buss 1988; Miller 2000; Caron 2002) and regarded by some as uniquely human (Bergson 1924; Caron 2002). Humor may have evolved to function as a coping mechanism. Freud (1960) posited that laughter served to discharge the accumulation of internal tension, an interpretation consistent with empirical observations of humor-induced stress reduction (Berk and others 1989). In clinical contexts, "laughter therapy" is used to increase pain tolerance (Weisenberg and others 1995) and immune function (McClelland and Cheriff 1997; Bennett and others 2003).

Humor also has a strong social aspect, and in fact, measurements of extroversion in human subjects have been found to correlate with humor-elicited activity in reward regions as measured by functional magnetic resonance imaging (fMRI) (Mobbs and others 2005). People are more likely to laugh when part of a crowd than in isolation (Fridlund 1991; Devereux and Ginsburg 2001; Smoski and Bachorowski 2003) and a "sense of humor" in an individual may help raise that individual's social status (Salovey and others 2000), increase that individual's social support network (Salovey and others 2000), facilitate pair bonding in romantic relationships (Ziv and Gadish 1989; Bippus 2000), and attract compatible mates (Murstein 1985; Buss 1988; Cann and others 1997; Miller 2000; Bressler and Balshine 2005; Bressler and others 2006). The role of humor in some of these social interactions has been proposed to differ according to gender (Ziv and Gadish 1989; Abel 1998; Smoski and Bachorowski 2003; Bressler and Balshine 2005; Bressler and others 2006), and, intriguingly, a recent fMRI study suggests differences in brain activity in men and women during the perception of humor (Azim and others 2005).

Presumably, the draw toward those who make us laugh is derived from the subjective pleasure that is inherent in a humorous experience. Recent imaging papers shed light on this aspect of humor by revealing that humor activates the ventral tegmentum and the ventral striatum (Mobbs and others 2003), as well as regions associated with emotion, such as the amygdala and insular cortex (Moran and others 2004). Thus, like the taste of fruit juice (Berns and others 2001), the sight of an attractive face (Aharon and others 2001; O'Doherty, Winston, and others 2003), or the scent of vanilla (Gottfried and others 2002), humor activates components of the system involved in reward processing. However, because humor differs from primary rewards in its cognitive complexity and abstract nature, we may also expect activity in "higher order" reward regions that mediate association formation and learning. Such regions are thought to be located in frontal cortex, such as the site of ventromedial activation observed by Goel and Dolan (2001), as well as frontal pole, where damage results in a disturbance in the affective response to humorous cartoons and jokes despite retention of the ability to discriminate humorous from nonhumorous stimuli (Shammi and Stuss 1999).

The rewarding aspect of humor is only part of the humor phenomenon, however. In order to appreciate a joke, you must first "get" the joke. What exactly is this cognitive mechanism that precedes the mirthful aspect of humor? Some researchers posit that humor requires an element of incongruity or cognitive conflict (Suls 1972; Coulson and Williams 2005). Indeed, an event related potential study by Coulson and Williams (2005) indicates that, compared with nonjoke stimuli, jokes presented to the left hemisphere elicit larger amplitude N400s, a hallmark of cognitive conflict. Although the slow time resolution of fMRI somewhat hampers the disentanglement of the cognitive from the rewarding aspects of humor, the study of Moran and others (2004) used popular television sitcoms as humorous stimuli to gain some insight into this question. They used the onset of a laugh track as a marker between humor comprehension and appreciation epochs. By observing activation 2 s prior to the onset of laughter, the authors found that brain activity during humor comprehension is distinct from that of humor appreciation and is characterized by left-lateralized activation in the left posterior temporal gyrus and left inferior frontal gyrus.

The affective dimension of humor appears to generalize across modalities; past studies have used both static and dynamic visual imagery (comics and film clips) to elicit humor, as well as auditory delivery of jokes. Some models (Suls 1972) predict that the reestablishment of coherence—that is, the process of discarding prior assumptions and reinterpreting the joke in a new context—is crucial to the comprehension of humor. If this is correct, then one should observe increased activation during the reinterpretation that is associated with the modality in which the humor is conceived. Goel and Dolan (2001) broached this question by observing activation associated with different types of auditory humor: semantic jokes and puns. They did indeed find differentiation between the 2 types of jokes. However, the anatomical sites of semantic and phonological processing are not always easily differentiated, which leaves this result open to interpretation.

In the present study, we used cartoons from "The Far Side" and "The New Yorker" to study brain activation specific to the type of humor portrayed. In cartoons containing language-independent "sight gag" humor, the humorous element is often a visually improbable predicament, social scene, or action that violates a viewer's initial expectations or assumptions. In cartoons containing language-based humor, the humor may be derived from incongruity between the picture and its descriptive caption or from a verbal deviation from social norms. Although both types of funny cartoons contain similar levels of complexity, make similar demands on the low-level visual system, and elicit similar feelings of mirth, the cognitive aspect of "getting the joke" differs depending on the sort of incongruity (sight vs. semantic) that needs to be reconciled. This in turn should lead to distinctly different activation patterns associated with the different types of humor. Inversely, both types of humor should produce the same affective result. Thus, as in previous studies, we expect both language-based and sight gag humor to increase activity in regions associated with reward and emotion, particularly the substantia nigra, nucleus accumbens, amygdala, and insular cortex.

The speculation that humor may be a uniquely human cognitive trait (Bergson 1924; Caron 2002) prompted our third hypothesis: humor will activate both anterior cingulate cortex (ACC) and frontoinsula cortex (FI), the 2 regions in which an evolutionarily recent neuron type, the Von Economo cells (previously termed "spindle neurons"), are present (Allman and others 2002, 2005). A review of the functional imaging literature reveals that the Von Economo cell regions, particularly FI, are active while reversal learning (O'Doherty and others 2001), decision making under uncertain conditions (Critchley and others 2001), and observing bizarre images of animal/object chimeras (Michelon and others 2003). Like humor, these paradigms involve incongruity detection and reappraisal and provided the impetus to formally test the hypothesis that humor activates the Von Economo regions ACC and FI.

Materials and Methods

Subjects

Twenty right-handed healthy volunteers (median age 26 years, range 20–61 years, 8 females) gave written consent to participate in this study. Four subjects were discarded from analysis for having 3or fewer ratings of "very funny" across all trials. All subjects were fluent English speakers and had normal or corrected to normal vision. None had a history of psychiatric illness, and they took no regular medication. The study was approved by the Caltech Internal Review Board.

Stimuli

Stimuli consisted of 100 line-drawing cartoons from The Far Side by Gary Larson (47 cartoons), or the New Yorker Magazine (various authors, 53 cartoons). Fifty of these drawings had been altered slightly so that the humorous element was removed—these were intended to serve as controls for those cartoons found to be humorous. In a preliminary study, we gathered funniness ratings on a scale of 1–10 for each drawing, both with and without captions. From this pilot study, we selected 25 "language-dependent" cartoons, which had mean ratings that were more than one standard deviation (SD) away from their original mean rating in absence of a caption. A total of 25 cartoons that were still within one SD from their mean rating after the caption was removed were categorized as sight gag stimuli, meaning that the humorous element was in the drawing itself, not the caption. Control groups of nonhumorous cartoons were selected for each category, language dependent and sight gag, so that the average number of words in the baseline (unfunny) group was not significantly different from the average number of words in the funny group. Thus, although each subject rated each cartoon separately, there were 50 canonically funny stimuli, as determined by the pilot study, and 50 canonically nonfunny control stimuli. Of the 50 canonically funny stimuli, half were language dependent and half were sight gag.

Task

The experiment consisted of an event-related design. Cartoons were presented in random order to subjects, with an interstimulus interval (ISI) of 300, 600, or 900 ms. We used this short ISI in order to avoid disrupting the "flow" of the humorous stimuli, which we feared might generate a feeling of impatience or anticipation in the subject. Studies suggest that, as long as the ISI is not fixed, using short ISIs can maintain sufficient statistical power in fMRI studies (Dale 1999; Friston and others 1999). Subjects were told to observe each cartoon and rate how funny they found it to be, any time after the "rating" cue appeared, 4 s after the stimulus onset. Ratings were done via button box, with 1 being very funny, 4 being "not funny at all," and 2 and 3 indicating that it was somewhere in between (note that, due to the limitations of the button box, this rating scale is different from the 1–10 scale used in the pilot study).

Imaging Procedure

The functional imaging was conducted by using a 3-T Siemens Trio magnetic resonance imaging (MRI) scanner to acquire gradient echo T_2*-weighted echo-planar images with blood oxygenation level-dependent (BOLD) contrast (time repetition = 2 s, echo time = 30 ms, flip angle = 90 degrees). Each functional volume consisted of 32 axial slices of 3.2 mm thickness and 3 mm in-plane resolution. Axial slices were acquired 20 degrees above the anterior commissure-posterior commissure line for each subject to minimize distortion and dropout in the orbitofrontal cortex area. A T_1-weighted structural image was also acquired for each subject using an magnetization prepared rapid gradient echo sequence (Siemens, New York, NY).

Imaging Analysis

The images were analyzed using statistical parametric maps (SPM2) (Wellcome Department of Imaging Neuroscience, London, UK, http://www.fil.ion.ucl.ac.uk/spm/). In order to correct for subject motion, the images were realigned to the first volume. Slice timing correction was applied, and images were spatially normalized to a standard Montreal Neurological Institute (MNI) template. Spatial smoothing was applied using a Gaussian kernel with a full width at half maximum of 8 mm. Following preprocessing, statistical analysis was carried out using a general linear model, in which each interval (stimulus onset to response time) was convolved with a canonical hemodynamic response function. Analysis of the subjects' behavior indicated that reaction times for an intermediate score (3 on the scale of 1–4) were significantly longer ($P < 0.05$), possibly because of the cognitive effort required to assign a score in this intermediate range. For this reason, only those cartoons which were rated with a 1 (least funny) or a 4 (most funny) by the subject were contrasted when exploring the main effect of humor, although all 4 scores were included as regressors. We additionally undertook a parametric analysis, in which linear increases in BOLD activation were correlated with the subjective rating of each image.

To look at modality-specific activation, we compared activation during the language-dependent funny cartoons and the visually funny cartoons (25 each), as determined in the pilot study, versus 2 matched unfunny cartoon control conditions (25 each). Control cartoons were selected for each group so that the average number of words in the cartoon did not differ significantly between funny and nonfunny control conditions. Head movements as determined by the motion correction–preprocessing step were used as regressors of no interest. We performed a two-way analysis of variance (ANOVA), which allowed us to parse the main effects of cartoon humor (funny vs. not funny), the main effects of cartoon type (visual vs. verbal), and the interaction between the 2 factors. To identify directionality of the response [i.e., (language-modulated humor) > (visually modulated humor) and vice versa], we subsequently performed *t*-tests. We additionally calculated the difference in betas $[(\beta_{\text{language humor}} - \beta_{\text{language controls}}) - (\beta_{\text{visual humor}} - \beta_{\text{visual controls}})]$, and vice versa, for each subject at the peak voxel for each of these contrasts in order to generate the population means (Fig. 6). To determine the betas at these voxels, the peak voxel from each of the two second-level *t*-tests was used as the center of a sphere with a radius of 10 mm. For each individual, we then found the peak voxel within this sphere and recorded the betas for all 4 regressors to determine population means.

Regions of activity were determined using a human brain atlas (Duvernoy 1991). The SPM-based toolbox MarsBaR (Brett and others 2002) was used to perform region of interest (ROI) analyses. We used canonical, MNI atlas–based ROIs for corrections of the caudate, putamen, and globus pallidus. Small-volume correction for nucleus accumbens was accomplished by centering a sphere of 6.4 mm radius (based on reports that the mean volume of the structure is 1.1 cc in a group of normal human controls [Deshmukh and others 2005]) at the coordinates (6, 2, −4) and (−6, 2, −4) as reported by Mobbs and others (2003). A ROI for ACC was delineated in order to approximate Brodmann's area (BA) 24. We drew a line connecting the genu and splenium on an average image created from the 16 normalized anatomical images. The extension of a perpendicular at the midpoint of this line across the cingulate cortex marked the posterior boundary of our anterior cingulate ROI. In the case of FI small-volume correction, nnormalized anatomical scans for each individual were imported

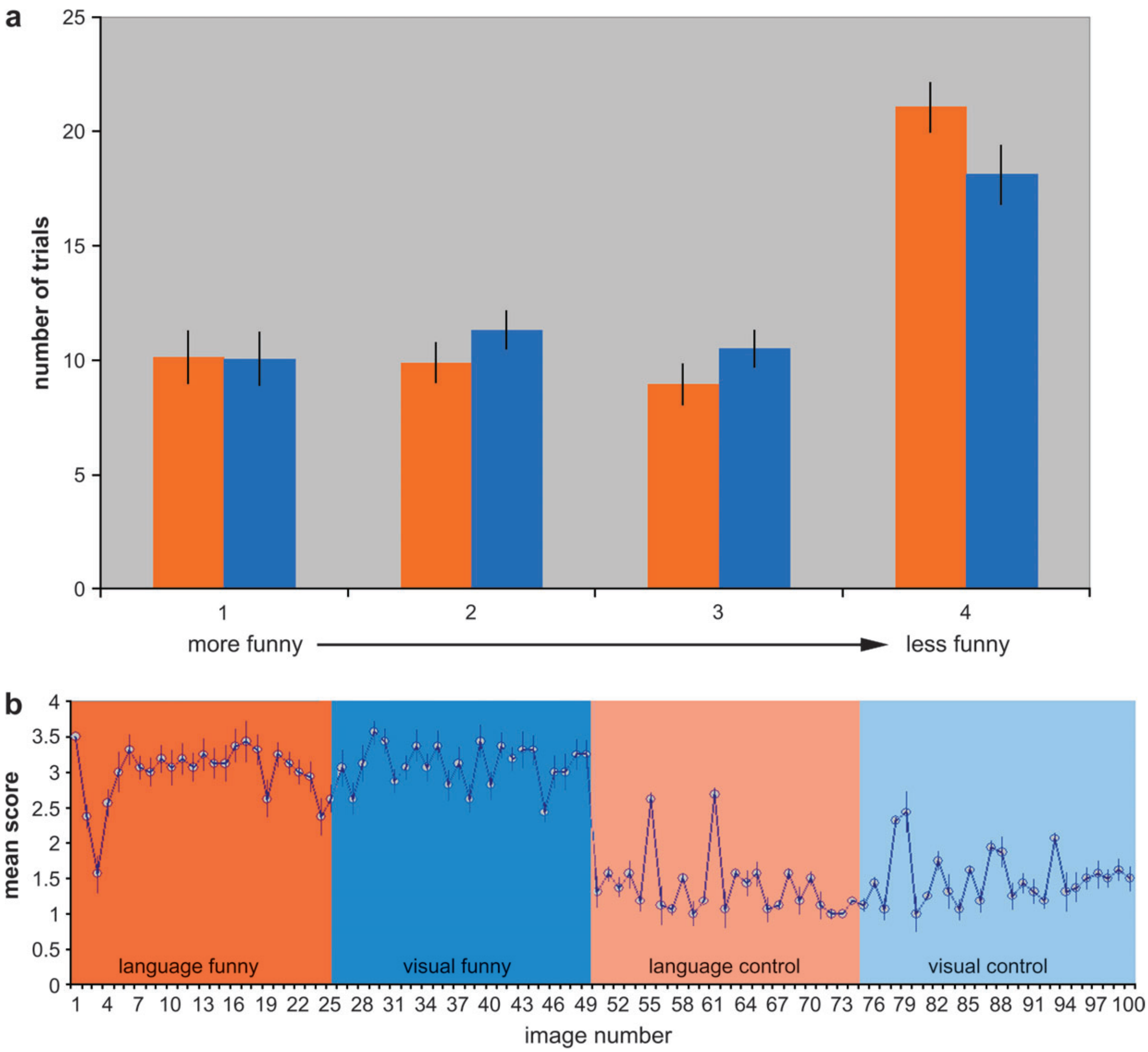

Figure 1. (*a*) Mean distribution of trial types across rating (1–4, with 4 being the most funny) and category (language-based, red; visual, blue;) for all 16 subjects. (*b*) Mean score (1–4, with 4 being the most funny) for each cartoon, computed across the 16 fMRI subjects. Cartoons 1–25 (red block) were canonically funny language cartoons, as determined in the pilot study, and cartoons 26–50 (blue block) were canonically funny visual cartoons. Cartoons 51–75 (pink block) were control language cartoons, whereas cartoons 76–100 (light blue block) were control visual cartoons. Note the relatively low mean scores of the control cartoons relative to funny cartoons.

into MRIcro. The experimenter with extensive experience in locating region FI in human brain histology preparations (John M. Allman) demarcated region FI on each anatomical scan. Normalizing and then averaging these images provided a ROI used for small-volume correction in MarsBaR.

Results

Behavior

Four subjects were discarded from analysis for having 3 or fewer ratings of very funny across all trials. Across the remaining 16 subjects, 19% of cartoons were scored as "very funny" and 40% scored as "not funny at all." Of those cartoons rated very funny, about half were Far Side (mean 46.3%, 10.9 SD). Neither was there a significant difference in ratings between Far Side and New Yorker cartoons (Far Side mean rating = 1.82, 0.28 SD; New Yorker mean rating = 1.80, 0.21 SD) nor was there a significant difference in the number of language and the number of visual cartoons selected as funny (P = 0.90; Fig. 1*a*). Mean ratings for the canonically humorous cartoons (as determined in the pilot study) were significantly higher than the mean ratings for control cartoons ($P < 0.01$, Fig. 1*b*). Mean ratings for language-dependent and visual cartoons were not significantly different. Reaction times (mean 7.04 s, 2.95 SD) for cartoons rated very funny and not funny at all were not significantly different, though reaction times for an intermediate score of 3 on a 1–4 scale were significantly higher.

Functional Imaging

As predicted, comparison of the humor versus control states revealed activation in both of the Von Economo cell regions: bilateral FI (right, $P < 0.03$; left, $P < 0.01$; corrected for multiple comparisons across a small volume of interest) and left ACC ($P <$ 0.03 corrected for multiple comparisons across a small volume of interest) (Fig. 2). Additional activation was similar to that reported earlier, namely, an extended network involving the limbic system and reward areas: bilateral putamen, bilateral nucleus accumbens, and left insula all survived small-volume correction ($P < 0.05$).

The parametric analysis, which we undertook to explore which areas of activity covaried with the funniness ratings, yielded results similar to those of the funny versus unfunny contrast described above. Regions of covariance included bilateral superior temporal sulcus, substantia nigra, and caudate, left putamen, left superior frontal gyrus, including dorsolateral prefrontal cortex, and left hippocampus and entorhinal cortex

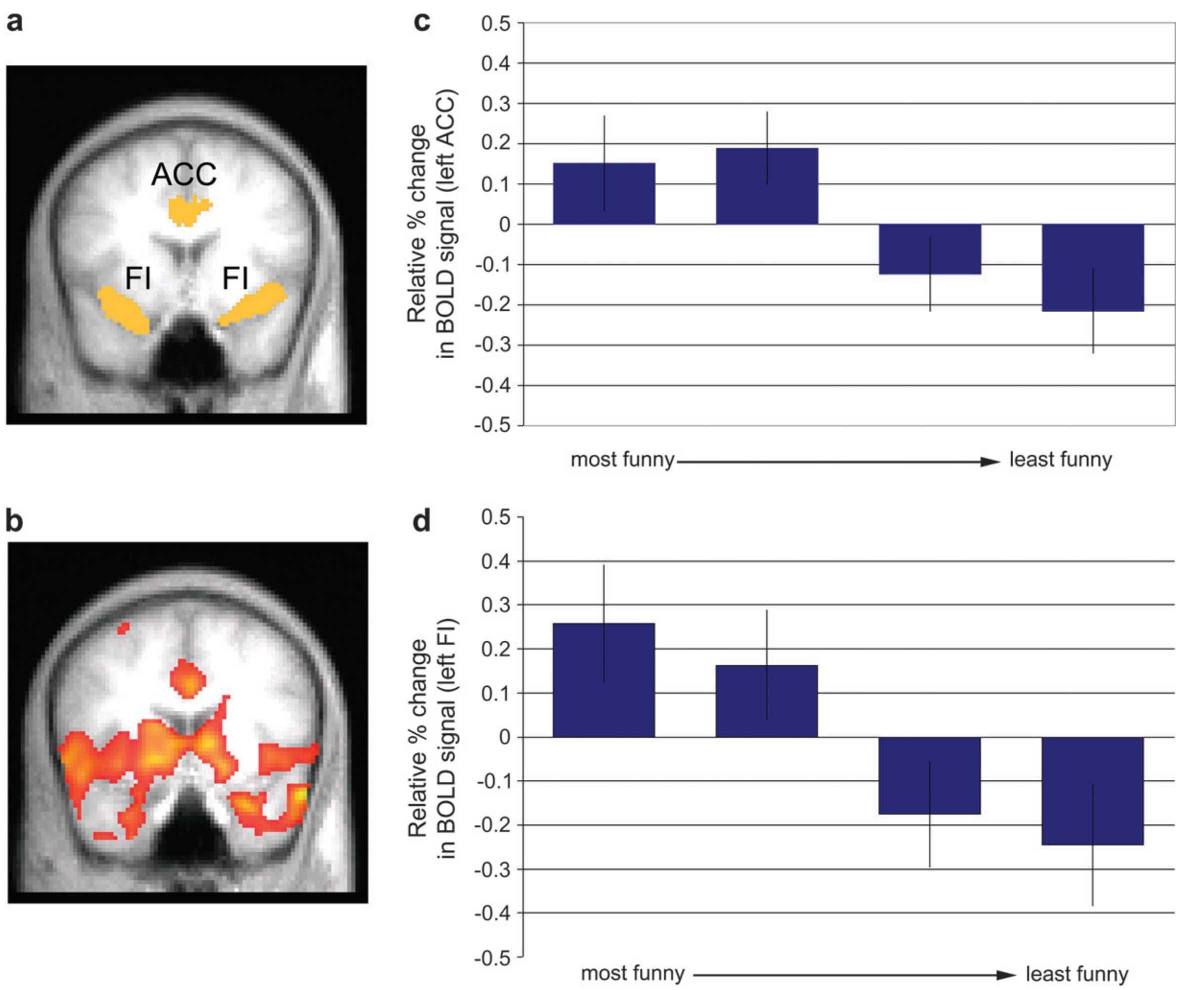

Figure 2. (*a*) Coronal view of ACC and FI cortex ROIs (yellow) overlaid on an average of the subjects' anatomical images. (*b*) Coronal slice showing regions with significant ($P < 0.001$, uncorrected) increases in activity with increasing ratings of funniness. (*c*) Relative percent change in ACC across all subjects. Error bars represent standard error of the mean (SEM). (*d*) Relative percent change in FI across all subjects. Error bars represent SEM.

($P < 0.0005$; Table 1). Bilateral ACC, FI, and insula proper all survived small-volume correction for the parametric model ($P < 0.03$), as did caudate, putamen, nucleus accumbens, and amygdala (Figs 2 and 3). Using a two-way *t*-test, we found sex differences in the parametric response similar to those found by Azim and others (2005), with women having greater activity in the middle frontal gyrus, inferior temporal lobe, posterior cingulate, and fusiform gyrus, among other places ($P < 0.005$ uncorrected; Supplementary Figure 1). There were no regions with significantly greater activity in men compared with women.

A two-way ANOVA revealed the differences in activity due to the main effects of humor, the main effects of humor type, and the interaction between these 2 factors (Fig. 4). Interaction effects between the language-dependent and sight gag humor categories revealed the functional dissociation between the 2 different types of humor (Figs 5 and 6 and Tables 2 and 3). Activity that was elicited by language-based humor compared with visual humor included the middle temporal gyrus, the inferior frontal gyrus, and the inferior temporal gyrus, regions functionally defined as Wenicke's area, Broca's area, and the basal temporal language area, respectively (Table 2) (Benson 1993; Just and others 1996; Friederici 2002). Application of a liberal probability threshold ($P < 0.05$, uncorrected for multiple comparisons), suggested a more extended region of activity in the middle temporal gyrus that extended up to the length of the temporal lobe (Supplementary Figure 2). In contrast, the reverse comparison [(visually funny cartoons – visual controls) > (language-based funny cartoons – language controls)] activated broad swaths of bilateral higher order visual cortex, including the horizontal posterior segment of the superior temporal sulcus, the middle occipital gyrus, and the precuneus (Table 3 and Figs 5 and 6).

Analysis of the conjunction of the 2 humor types [(language humor – language controls) ∩ (visual humor – visual controls), all thresholded at $P < 0.005$, cluster size > 20] revealed activity in several hedonic regions, including the midbrain and amygdala (Table 4 and Fig. 7).

Table 1
Brain regions that display increasing activation with increasing scores of "funniness" ($P < 0.0005$)

Brain region	L/R	Coordinates (*x*, *y*, *z*) of peak voxel	*Z*-score
Superior temporal sulcus	L, R	−48, −60, 20	5.56
Middle temporal gyrus	R	56, 12, −22	5.45
Substantia nigra	R, L	6, −6, −12	5.36
Superior parietal gyrus	L	−2, −56, 46	5.09
Hippocampus	L	−60, −14, −22	4.78
Entorhinal area	L	−30, −4, −30	4.7
Superior temporal gyrus	L, R	−58, 14, −8	4.68
Superior frontal gyrus	L	−6, 56, 36	4.64
Head of caudate	L, R	−6, −2, 12	4.62
Putamen	L	−18, 6, −4	4.51
Mid cingulate gyrus	R	2, 10, 32	4.45

Discussion

The results reported here demonstrate the disparate mechanisms underlying the euphoric and cognitive aspects of humor. Specifically, we show that language-dependent cartoons elicit activity in classical language areas in the left temporal lobe, whereas sight gag cartoons elicit activity in higher order visual areas. We additionally demonstrate that both types of humor result in increased activity in reward- and emotion-related areas, including the nucleus accumbens and the amygdala.

The two-stage model of humor consists of an initial recognition of incongruity (surprise) and the subsequent reinterpretation of the incongruent situation into a coherent whole

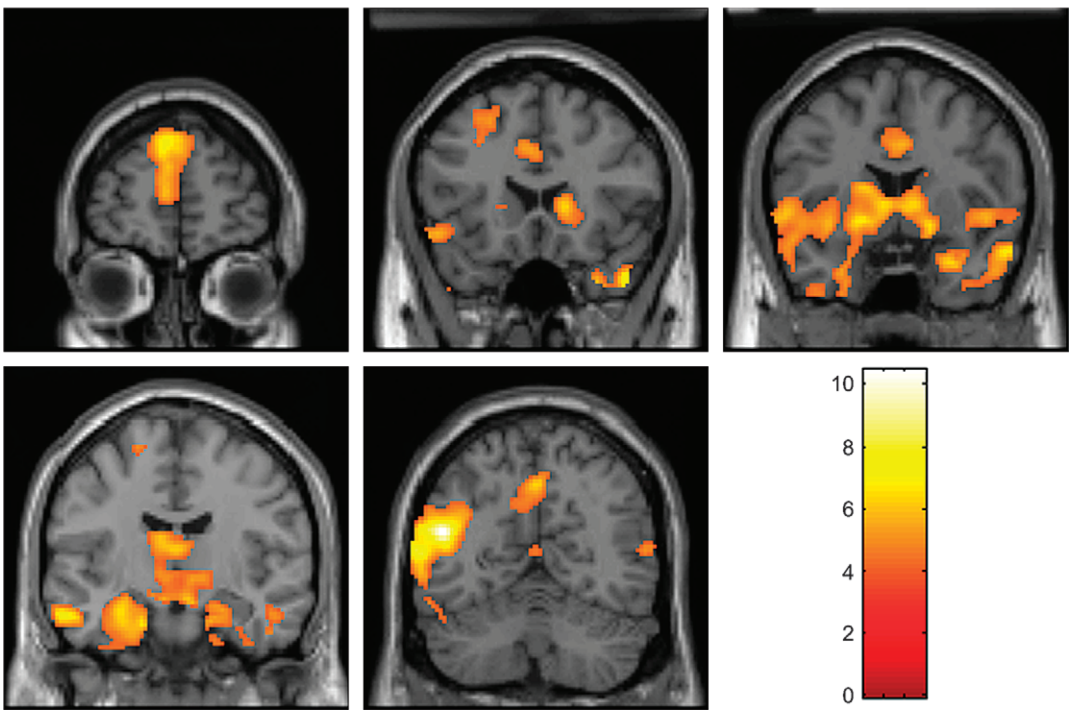

Figure 3. Coronal views of group contrast map for activity that correlates linearly with cartoon rating (increased activity with higher rating of funniness).

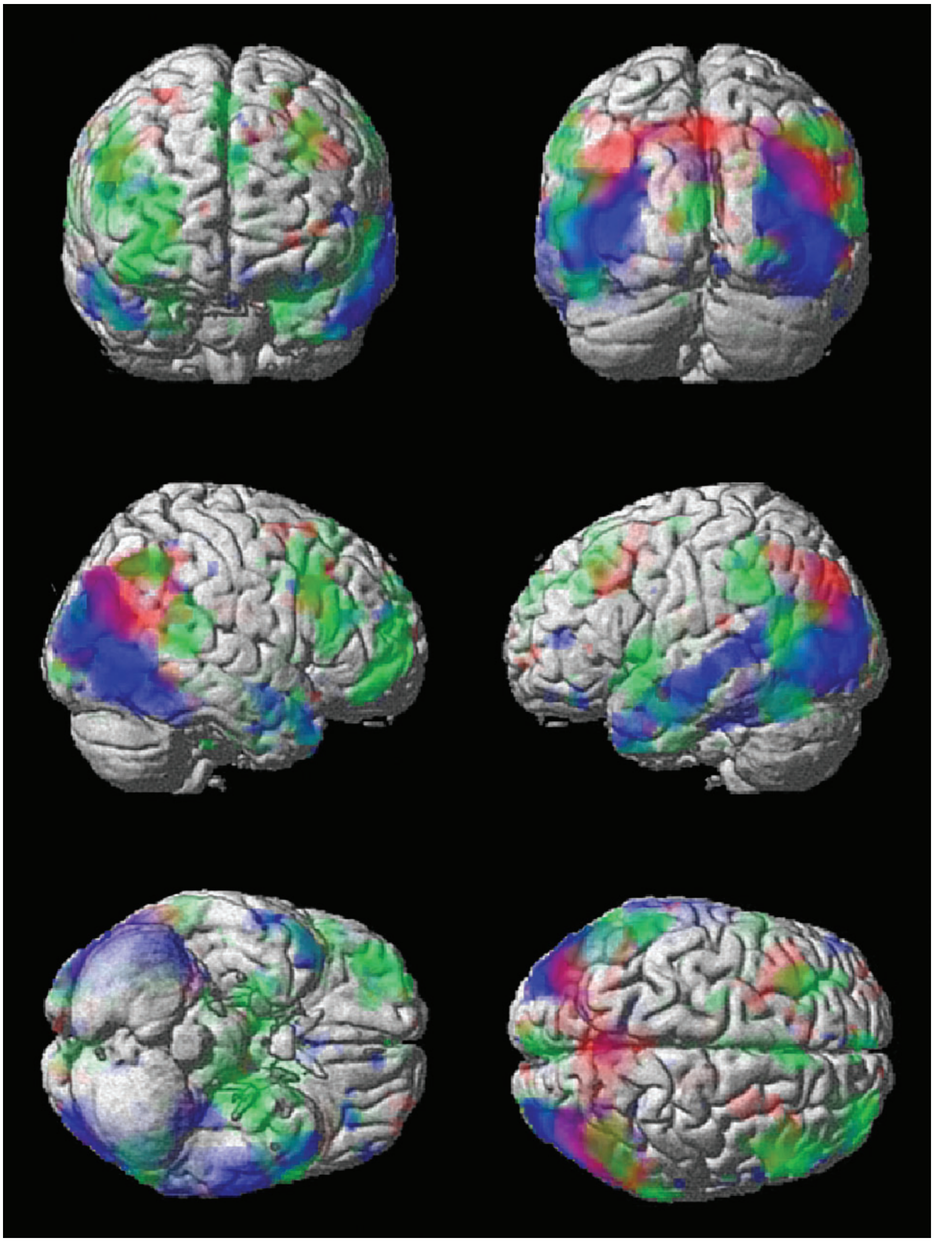

Figure 4. Surface projections of color-coded SPMs showing the results of a two-way ANOVA ($P < 0.005$, uncorrected) overlaid onto canonical single subject anatomic rendering. Green indicates the main effect of humor (humorous cartoon vs. control), blue indicates the main effect of cartoon type (language vs. visual), and red indicates regions for which there is an interaction between these two effects. Violet indicates the regions that show variations in activity according to cartoon type (language vs. visual) as well as to the interaction. Trials were parsed into categories (funny or not funny, visual or language, 25 trials of each type) in a canonical fashion for all subjects.

(framework shifting) (Suls 1972). This suggests that the details relevant to the humor require additional processing, possibly engaging feedback loops between lower level sensory areas and regions in frontal cortex associated with attention and executive function. Consistent with this model, our data show that cognitive processing during the experience of humor is domain specific, with increased activation in the modules most relevant to the element from which the humor is derived.

Sight gag humor is dependent on visual incongruities between several elements in the cartoon. Functionally, our results show that the processing of sight gag humor shows increased activation in higher order visual regions bilaterally when compared with language-dependent humor, consisting of a large expanse of extrastriate regions beyond V2 (Tootell and others 1996). Interestingly, areas V1 and V2 are not more active during the funny cartoons than they are during the nonfunny cartoons, suggesting that the activation elicited by visual humor is a result of top–down modulation, rather than an increase in sensory stimulation per se. The strongest sites of activation were the precuneus and dorsolateral prefrontal cortex (BA 9/46), anatomically known as middle frontal gyrus. These 2 regions are associated with visual imagery (Ishai and others 2000), contextual associations (Linden and others 2003; Lundstrom and others 2005; Rorie and Newsome 2005), and conscious awareness of visual stimuli (Kjaer and others 2001). Evidence also exists that the precuneus is active during paradigms that

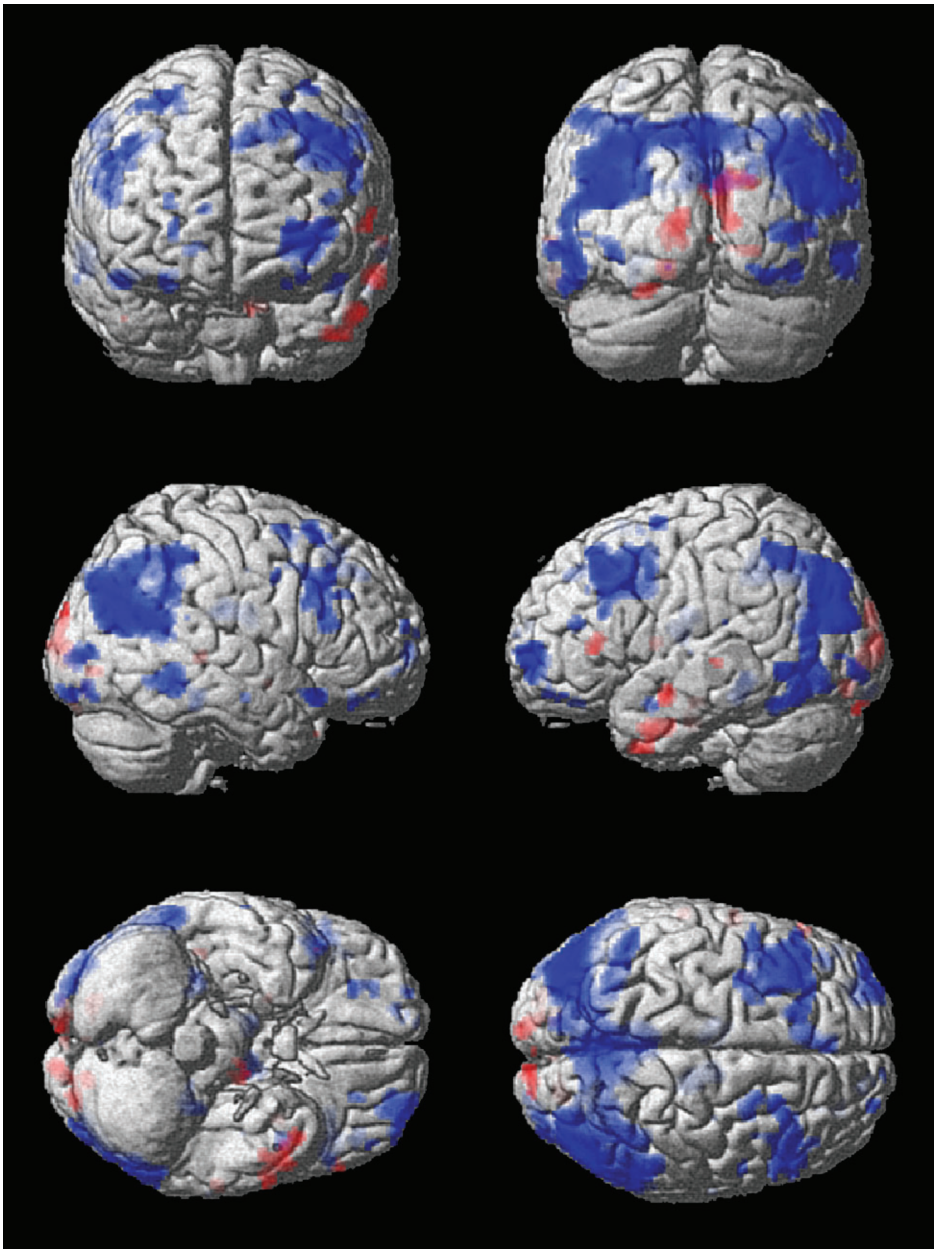

Figure 5. Surface projections of color-coded SPMs showing the results of second-level *t*-tests ($P < 0.005$, uncorrected) overlaid onto canonical single subject anatomic rendering. Blue indicates those regions where [(visual humor – visual control) > (language-based humor – language-based control)]; red indicates the opposite.

require varied perspective taking (Ruby and Decety 2001; Jackson and others 2006) or the recruitment of theory of mind (Gallagher and others 2000), cognitive mechanisms that are similar to the reinterpretation step that precedes "getting" a joke.

Interaction between frontal regions and stimulus-specific regions in the temporal lobe are thought to underlie recognition for faces (Haxby and others 1994; Kanwisher and others 1997) and objects (Riesenhuber and Poggio 2002). Our results are analogous with this, as frontal regions and higher visual areas act reciprocally to place the cartoons' visual elements into a sensible context. This requires various inferences about spatial and conceptual relationships between objects based on information-sparse line drawings. This cognitive effort results in the relative activation of both the parietal "where" stream as well as the temporal "what" stream of visual processing, both of which act in concert with frontal regions that integrate this processing and hold relevant information in working memory (Ungerleider and Haxby 1994).

Activation that is present during language-dependent humor as opposed to sight gag humor is located in left-lateralized temporal and frontal cortices. Left hemispheric damage has been long associated with language deficits in regions associated with language processing, and the regions activated by language-dependent humor correspond strongly to classical language areas, including Broca's area, anatomically described at inferior frontal gyrus; Wernicke's area, including middle temporal gyrus and superior temporal sulcus; and the basal temporal language areas located in inferior temporal gyrus (Benson 1993; Just and others 1996; Friederici 2002). Surprisingly,

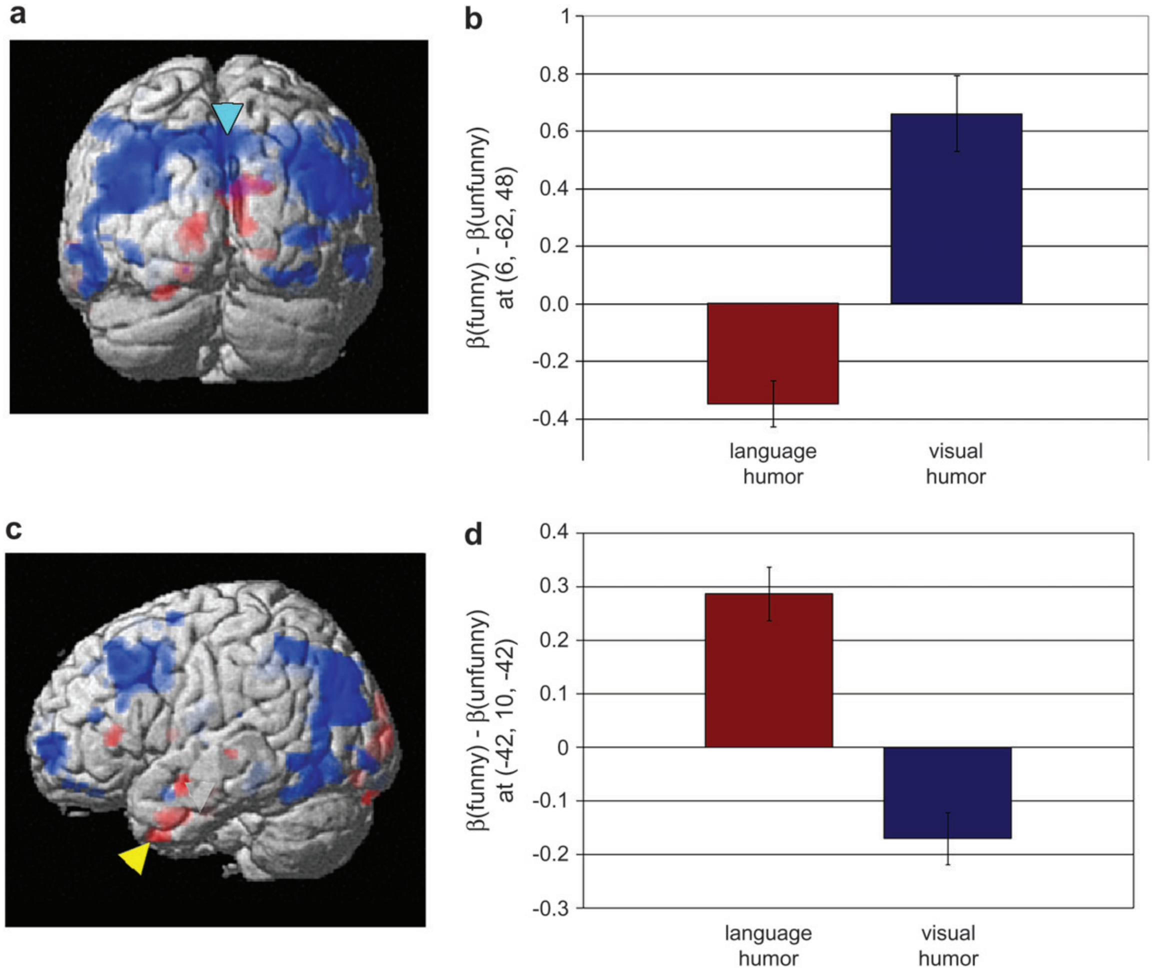

Figure 6. (*a*) Replication of surface projection from Figure 4, with peak voxel modulated by visual humor > language humor indicated by the cyan arrowhead. (*b*) Mean differences in betas across all subjects for the voxel indicated in (*a*). Red bar, differences in betas for funny trials minus the betas for control trials for language-based cartoons; blue bar, differences in betas for funny trials minus betas for control trials for sight gag cartoons. (*c*) Replication of surface projection from Figure 4, with peak voxel modulated by language humor > visual humor indicated by the yellow arrowhead. (*d*) Mean differences in betas across all subjects for the voxel indicated in (*c*). Red bar, differences in betas for funny trials minus the betas for control trials for language-based cartoons; blue bar, differences in betas for funny trials minus betas for control trials for sight gag cartoons. Note differences in *y*-axis scale between (*b*) and (*d*). Error bars represent standard error of the mean in both graphs.

Table 2

Atlas coordinates (in MNI space) and *Z*-scores of peak activation during the cartoon task for the interaction between the sight gag and language-dependent categories

Brain region	L/R	Coordinates (*x*, *y*, *z*) of peak voxel	*Z*-score
Inferior temporal gyrus	L	−42, 10, −42	3.75
Middle temporal gyrus	L	−52, 4, −32	3.31
Inferior temporal sulcus	L	−50, −4, −30	3.18
Superior occipital gyrus	R	4, −98, 20	3.53
Superior occipital gyrus	R	12, −98, 28	3.10
Cuneus	L, R	14, −98, 8	3.00
Transverse occipital sulcus	L	−14, −94, −2	2.78
Fourth occipital gyrus	L	−14, −86, −14	3.27
Inferior frontal gyrus, pars triangularis	L	−58, 32, 6	3.18
Superior temporal sulcus	L, R	−64, −26, 0	3.10
Inferior occipital gyrus	L, R	−24, −92, −22	3.07
Subiculum	L	−14, −16, −20	3.03
Parahippocampal gyrus	L	−10, −14, −28	2.86
Short insular gyrus	L	−32, 2, 8	2.82

Note: Regions for which [Language-dependent humor (funny − unfunny) > sight gag humor (funny − unfunny)], that is, regions of activation for which language-based humor is significantly greater than sight gag humor have been listed (all comparisons $P < 0.005$, uncorrected, cluster > 10 voxels).

language-dependent humor also elicited activation increases in the region of the occipital lobe corresponding to the primary visual areas. This could arise either from increased visual input during language humor, for example, from a relatively large search pattern that includes both the caption and the picture, or from a relative suppression in primary visual activity during visual humor.

Although it is clear that a dissociation exists between the mechanisms that underlie different forms of humor, our results also emphasize the common features that characterize various types of humor. Our study replicates the results of past studies (Mobbs and others 2003) that found heightened activity in a network of subcortical regions including the nucleus accumbens and substantia nigra, thought to underlie the hedonic aspect of humor. For most regions, this was true not only for an investigation of the main effect of humor but also for a parametric analysis (observing correlations of activity in these regions with varying levels of reported amusement) and for a conjunction analysis between the 2 different types of humor (visual and language-based). This further strengthens the

Table 3
Atlas coordinates (in MNI space) and Z-scores of peak activation during the cartoon task for the interaction between the sight gag and language-dependent categories

Brain region	L/R	Coordinates (x, y, z) of peak voxel	Z-score
Precuneus	R	6, −62, 48	5.03
Superior temporal sulcus, horizontal posterior segment	L, R	−38, −76, 20	4.94
Middle frontal gyrus	L, R	−36, 26, 44	4.70
inferior temporal gyrus	R	60, −48, −10	4.60
Inferior frontal gyrus	L, R	−30, 62, 0	4.60
Anterior orbital gyrus	L	−28, 52, −16	3.38
Superior temporal gyrus	R	48, 20, −18	4.41
Frontoinsula	R	38, 18, −14	2.72
Superior frontal sulcus	R	26, 18, 62	3.42
Middle occipital gyrus	L	−38, −90, −4	3.87
Anterior orbital gyrus	R	26, 38, −20	3.70
Middle frontal gyrus	R	42, 24, 38	3.50
Inferior occipital gyrus	R	38, −86, −14	3.43
Fourth occipital gyrus	R	32, −94, −14	3.39
Thalamus	L	−8, −12, 16	3.39
Fusiform gyrus	L, R	−26, −40, −8	3.38
Posterior cingulate gyrus	R	6, −48, 24	3.21
Lateral occipital sulcus	R	38, −90, 2	3.20
Lateral orbital gyrus	L	−46, 46, −18	3.11

Note: Regions for which [Sight gag humor (funny − unfunny) > language-dependent humor (funny − unfunny)], that is, regions more strongly activated by sight gag humor than by language-based humor have been listed (all comparisons $P < 0.005$, uncorrected, cluster > 10 voxels).

Table 4
Atlas coordinates (in MNI space) and Z-scores of peak activation from a conjunction analysis of both visual humor and language-based humor [(language funny − language unfunny) AND (visual funny − visual unfunny)]

Brain region	L/R	Coordinates (x, y, z) of peak voxel	Z-score
Midbrain	L	−10, −24, −12	4.61
Amygdala	L/R	−28, −4, −30	4.13
Hippocampus	L	−22, −24, −12	3.93
Fusiform gyrus	L	−48, −56, −20	3.78
Superior temporal sulcus	L/R	66, −40, 10	3.54
Middle temporal gyrus	L	−60, −54, 2	3.39
Hypothalamus	R	8, −4, −8	3.31
Subiculum	R	14, −28, −6	3.19
Nucleus accumbens	L	−12, 4, 6	2.88
Inferior temporal gyrus	R	32, −6, −40	2.87
Entorhinal area	R	28, 0, −34	2.85
Inferior frontal gyrus	L	−60, 12, 2	2.83

evidence that humor acts similarly to primary rewards via the mesolimbic dopaminergic system. We also observed amygdala activity in both the parametric and main-effects analyses, which corroborates past results (Mobbs and others 2003; Moran and others 2004). Recent evidence supports a role for amygdala in the processing of rewards as well as aversive events (for review, see Baxter and Murray 2002), and animal lesion studies show that an intact amygdala is necessary to link an object to a current (as opposed to consistent) reward value. Amygdala activity may thus relate to the "reinterpretation" step in the Suls model and the associated update of the cartoon's value. Another interpretation of the amygdalar activity relates to the observation that patients with bilateral amygdala lesions fail to show normal changes in skin-conductive response (SCR) in a gambling task (Bechara and others 1999). Changes in somatic markers such as SCR may be concomitant with, or a crucial feature of, humor, a phenomenon that could explain the observed activity in both the amygdala and the hypothalamus.

Regions of the brain highlighted in the conjunction analysis of language-based and sight gag humor may reflect cognitive demands common to processing both types of humorous cartoons in addition to the hedonic component of humor. For example, our conjunction analysis revealed activity in the superior temporal sulcus and middle temporal lobe, regions associated with face perception (Desimone 1991) and with the processing of social informational cues such as the assessment of gaze and head direction (Perrett and others 1985). Inferior temporal gyrus is known to be associated with the semantic retrieval processes that occur when viewing line drawings (Mazard and others 2005), and the hippocampus is also postulated to have a role in semantic processing under conditions of lexico-semantic ambiguity (Hoenig and Scheef 2005). In all these cases, it is likely that we are seeing heightened processing of relevant stimuli in the funny cartoons in comparison with the nonhumorous control cartoons, analogous to the increased activity we report in domain-specific areas during the processing of language-dependent or sight gag cartoons.

We also report in this study that humorous cartoons activate the 2 regions in the human brain known to have Von Economo cells (von Economo and Koskinas 1929), a specialization in neuronal morphology that has evolved in the last 15 million years (Nimchinsky and others 1999; Allman and others 2002, 2005). Furthermore, we show that the BOLD response in these 2 regions, ACC and FI, is correlated with the subjective rating of funniness (see Fig. 2). Humor involves both uncertainty (during the initial appraisal of the humorous situation) and sociality (via laughter or other social signals), both of which have been shown to elicit activity in ACC and FI (Shin and others 2000; Critchley and others 2001; O'Doherty, Critchley, and others 2003; Bartels and Zeki 2004; Singer, Kiebel, and others 2004; Singer, Seymour, and others 2004). We propose that the ability to appreciate humor is related to the ability to make rapid, intuitive assessments, a skill that would be particularly adaptive during the complex social interactions typical of the hominoids and that the von Economo cells are a phylogenetic specialization in the circuitry that underlies such fast and intuitive decisions. It is the convergence of this fast intuition with a slower, deliberative assessment that creates the cognitive mismatch upon which humor is based. A listener "gets" a joke the moment that the initial intuitive interpretation is updated, thus providing the input required to "recalibrate" ACC and FI. We propose that a similar mechanism enables fluent social interaction. This is consistent with a recent study using a placebo paradigm, which suggests that the ACC and orbitofrontal cortex modulate expectation in a top–down manner (Petrovic and others 2005). Another interpretation involves the regions' roles in mediating the autonomic changes that are likely to be induced by humor (Critchley and others 2001; Critchley 2002). Again, this is consistent with the activity we observed in the amygdala and hypothalamus, both of which have descending projections to autonomic output nuclei. Critchley suggests that these 2 regions play a primary role in mediating autonomic changes. These various explanations are not mutually exclusive because the changes in expectation that occur during humor are likely to be associated with fluctuations in anticipatory arousal states. This could be the physiological correlate of the "release of tension" humor mechanism proposed by Freud (1960).

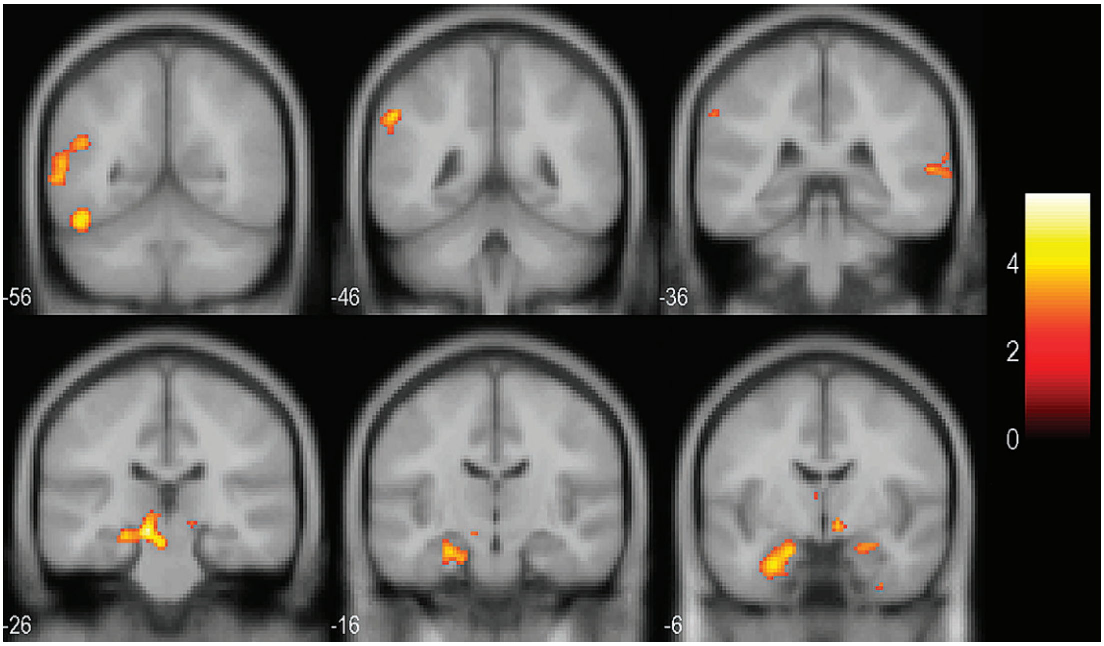

Figure 7. Coronal view of activity elicited in both language-dependent humor (funny – control) and visual (funny – control) humor ($P < 0.005$, uncorrected, for both).

Supplementary Material

Supplementary figures can be found at: http://www.cercor.oxfordjournals.org/.

Notes

We would like to thank R. McKell Carter and John O'Doherty for their comments on the manuscript. This work was funded by the David and Lucille Packard Foundation, the Gordon and Betty Moore Foundation, and the Swartz Foundation. *Conflict of Interest*: None declared.

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